

CRANIAL MORPHOLOGY OF THE LOXOMMATIDAE
(AMPHIBIA : LABYRINTHODONTIA)

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[Plates 1 and 2]

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The labyrinthodont superfamily Loxommatoidea is now divided into two families. The highly aberrant *Spathicephalus* is placed in a new family, the Spathicephalidae, to be described elsewhere. The family Loxommatidae is retained for the remaining genera, *Loxomma*, *Megalocephalus* and *Baphetes*.

Additional material and further preparation has made possible a redescription of the three loxommatid genera and new skull restorations have been produced for most species. In particular the loxommatid braincase and palatoquadrate are reconstructed for the first time; in many features their structure is more primitive than that hitherto described for any temnospondyl.

Since an intertemporal bone is found to be a feature of *Baphetes* as well as *Loxomma*, these two genera have been separated on the basis of skull shape and on stratigraphical grounds. A specimen from the Communis zone, Westphalian A, is attributed to *Loxomma*, as *L. rankini* sp.nov., while '*Loxomma bohemicum*' has been transferred to the genus *Baphetes* as *B. bohemicus* (Fritsch). A further specimen, originally associated with *Macrerpeton*, has also been referred to this genus as *B. lintonensis* sp.nov.

The skull of *Megalocephalus pachycephalus* can be described in greater detail than that of any other loxommatid species and thus forms the basis for discussion of the functional morphology. Jaw muscles are reconstructed for this species and it is concluded that the antorbital vacuity, which characterizes the Loxommatoidea, evolved as a bulging hole for a large pterygoideus muscle associated with a piscivorous habit and a kinetic inertial system of jaw closure.

Consideration of the mechanics of jaw closure sheds light on a further enigma, i.e. the function of the basipterygoid articulation in the primitive temnospondyl skull. The loxommatid skull is considered divisible into two units. The presence of a specialized cranial joint between the quadrate and quadratojugal allows potential for any movement at the basal articulation to be accommodated in the main at this site. It is suggested that the system described for loxommatids represents an alternative design to the mobile cheek region of anthracosaurs and that the articulations represent zones of elasticity, which accommodate the stresses on the skull caused by a powerful jaw musculature.

INTRODUCTION

The Loxommatoidea were a group of large aquatic labyrinthodont Amphibia from the coal swamp lake systems. They are recorded from a number of localities in the British Carboniferous, which range in geological time from the Carboniferous Lower Limestone group of Scotland to the Upper Coal Measures, and also from Carboniferous horizons of Europe and North America.

The majority of specimens described here were discovered during the latter part of the nineteenth century. The major pioneer studies are those of Owen on *Baphetes planiceps* (1854; 1855), Huxley on *Loxomma allmanni* (1862) and a series of papers produced between 1864 and 1889 on specimens originally thought to be *Loxomma* but now attributed to the genus *Megalocephalus*, by a group of palaeontologists, including Hancock, Atthey and Embleton, centred on the Natural History Society at Newcastle upon Tyne.

The relationship between loxommatid genera was first recognized by D. M. S. Watson whose work, published from 1912 onwards, forms a basis for subsequent consideration of the group. Watson believed that embolomereous vertebrae were primitive and were characteristic of most Carboniferous Labyrinthodontia. He included loxommatids and anthracosaurs in his

Grade Embolomeri (1917) and in his description of the anthracosaur '*Palaeogyrinus*' (*Palaeoherpeton*) and the loxommatid '*Orthosaurus*' (*Megalocephalus*) (1926) he demonstrated that the members of this taxon shared a number of primitive skull characters.

In a paper normally dated 1929 Watson gave a detailed account of his superfamily Loxomoidia (corrected to Loxommatoidea by Baird (1962)), in which he included the four genera in a single family. *Loxomma allmanni* Huxley was redescribed and a specimen from the Upper Carboniferous of Airdrie, Lanarkshire, placed in the same genus, but as *Loxomma acutirhinus* sp. nov. Two British specimens were added to Owen's genus *Baphetes*, as new species *B. kirkbyi* and *B. latirostris*, both from the Westphalian of Scotland. Specimens of *Megalocephalus* were included in a single species as *Orthosaurus pachycephalus* Barkas. A new genus *Spathicephalus* was created for skulls from the Limestone coals at Loanhead, Midlothian, all material from this site being referred to *Spathicephalus mirus* Watson.

Romer (1947) considered the protorhachitinous vertebral type to be ancestral for labyrinthodonts and thus disagreed with Watson's scheme of amphibian evolution. He placed the Loxommatoidea in the Rhachitomi, believing that the group would eventually be found to possess rhachitinous vertebrae. Corroborative evidence has been provided by Baird (1957) who described part of a vertebral column with apparently rhachitinous intercentra associated with a skull of *Megalocephalus* from Linton, Ohio (figure 16b).

The present classification of the Loxommatoidea follows that of Romer (1966) but the superfamily is now divided into two families. The family Loxommatidae is retained for *Loxomma*, *Megalocephalus* and *Baphetes*, a conservative group with a skull pattern similar to that of primitive edopoid temnospondyls, but with modifications for a piscivorous habit, whilst the highly aberrant *Spathicephalus* is now placed in a separate family, the Spathicephalidae.

Only the skull morphology of the Loxommatidae will be dealt with here. *Spathicephalus* and loxommatid postcranial material will be described elsewhere.

PRESERVATION OF MATERIAL AND TECHNIQUES

A complete list of the material studied is given for each species at the beginning of the appropriate section. The following abbreviations are used for the institutions owning the material:

- A.M.N.H. Department of Paleontology, American Museum of Natural History.
- B.M.(N.H.) Department of Palaeontology, British Museum (Natural History).
- C.G.H. Narodni Museum, Prague.
- G.S. Institute of Geological Sciences (British Geological Survey).
- H.G. Hunterian Museum, Glasgow.
- H.M. Hancock Museum, Newcastle upon Tyne.
- I.N.M. Irish National Museum, Dublin.
- K.C. Geology Department, King's College, London.
- M.C.Z. Museum of Comparative Zoology, Harvard University.
- Pu. Geological Museum, Princeton University.
- R.S.M. Department of Geology, Royal Scottish Museum.
- S.M. Sedgwick Museum, Cambridge.

After their first appearance in the Late Viséan, loxommatids became more common throughout Upper Carboniferous strata and consequently are found in a variety of matrices.

Preservation in cannel and shale is often excellent, apart from the inevitable compression.

Both form a uniform fine grain matrix that is not unduly hard and could usually be removed mechanically by means of a Stensiö automatic mallet or mounted needles. Often, however, when the above techniques were employed there remained a thin covering of matrix, which obscured fine detail and could not be removed without damage to the delicate bone surface. For refined development an Industrial Airbrasive Unit was used (Stucker 1961). For removal of shales and cancellous 'Airbrasive' Powder No. 1, calcium dolomite, was found to be most suitable.

Some loxommatid material, such as the holotype of *Baphetes kirkbyi*, is preserved as natural moulds and was studied from latex casts. Occasionally Coal Measure specimens are found in which the bone has disappeared and the resultant mould has filled in naturally with another material. This has happened to a large *Megalocephalus* skull (I.N.M. 187) from Jarrow Colliery, Eire, the mould having infilled with a dark organic silt. The resultant cast lacks definition, as the material had almost certainly shrunk during formation so that little detail was apparent and further preparation was impossible.

Coal shales may grade into bands or lenses of ironstone and several loxommatid skulls have been found in such matrices. Although usually distorted they have often suffered less compression than material preserved in coal or shale and the *Megalocephalus* specimen from Coalbrookdale is the best example of a Carboniferous amphibian skull preserved in the round. The major problem with ironstone is that it presents a hard intractable matrix that is difficult to remove. In some cases a small cold chisel was used to cut down the matrix to within a safe margin of the bone, then the 'Airbrasive' machine, with a fairly coarse powder (S.S. White No. 3, aluminium oxide) was used to 'eat' into the hard layers of ironstone surrounding the specimen, facilitating its removal with a Stensiö mallet. The final cleaning of the bone surface was once more with the 'Airbrasive', but using the fine calcium dolomite powder as the abrasive agent.

A solution of Perspex in chloroform was used as an adhesive for mending breaks in specimens, and was diluted when required as a varnish to protect the bone surface.

GENUS *LOXOMMA* HUXLEY

Loxomma is the earliest known and seemingly the most primitive loxommatid genus. It is limited here to three species, all from Scotland, and ranging in geological time from the Viséan Lower Limestone Group to the Modiolaris zone of the Middle Coal Measures.

The following diagnosis is based entirely upon skull material. *Generic diagnosis.* Loxommatids with a high triangular skull (known midline length up to 240 mm) with pre-orbital region approximately half midline length. Orbit and antorbital vacuity about equal in length. Pre-maxilla long anteroposteriorly bearing eight teeth where known. Lachrymal reaches nostril. Skull table relatively large and square. Intertemporal bone present. Maxilla contacts quadrato-jugal, excluding jugal from skull margin. Palate without anterior vacuity.

LOXOMMA ALLMANNI HUXLEY 1862

Specific diagnosis. Owing to the paucity of material only the following comparisons can be made between the holotype skull and other species. Loxommatids of the genus *Loxomma* with squamosal forming anterior border of otic notch on dorsal and ventral skull surface. Supratemporal bone long and narrow.

Description of material

Holotype. R.S.M. 1950.56.2. Hind part of skull roof exposed ventrally; figured by Huxley (1862, pl. XI, fig. 1) and Watson (1929, p. 235, fig. 13). From the Gilmerton Ironstone, Gilmerton Midlothian, Scotland. Lower Limestone Group, Carboniferous Limestone, Viséan.

In addition to being the earliest known loxommatid, *L. allmanni* was also the first labyrinthodont to be described from the British Carboniferous. Apart from two tentative associations (see below) the species is known only from the holotype, part of the posterior region of a skull roof exposed from the ventral surface (figure 1*a*), but a small area of the dorsal skull table has been developed out to show the well-defined temnospondyl pit and ridge ornament (figure 1*b*).

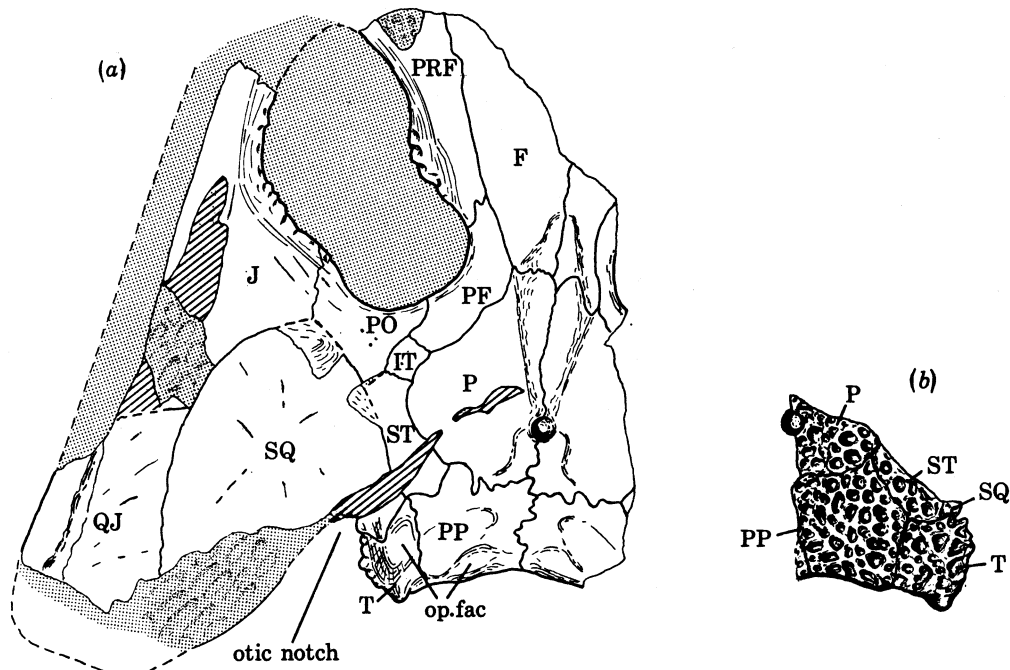


FIGURE 1. *Loxomma allmanni* Huxley, holotype skull. Half natural size: (a) ventral, (b) area of dorsal surface of skull table. Matrix stipple, broken bone hatched.

In most features *L. allmanni* resembles *L. acutirhinus*, for which a more complete description is possible (see below). The presence of a small inter-temporal bone is characteristic of the genus and although the maxilla has sheared off it apparently reached back to the quadratojugal. The braincase is also missing but areas for its attachment, similar to those described for *L. acutirhinus*, are apparent on the dermal roofing bones. The major difference between these two species is in the structure of the otic region. In loxommatids the rounded otic notch occupies the postero-lateral border of the skull table and is open posteriorly. In *L. allmanni* the supratemporal is excluded from the margin of the otic notch since the squamosal forms its anterior border on both surfaces of the skull roof (figure 1). In both the holotype of *L. allmanni* and the topotype of *L. acutirhinus* the pineal foramen is raised on a slight boss. This feature may be significant or could be an artefact of preservation.

Although a large number of specimens were attributed to the species *L. allmanni* during the latter part of the nineteenth century virtually all have subsequently been referred to the genus *Megalococephalus* (see below). An amphibian shoulder girdle was attributed to *Loxomma* by Huxley

(1862, pl. 11, fig. 2). The loxommatoid interclavicle is now known for *Megalocephalus* and *Spathicephalus* (Tilley (Beaumont, 1971)), and both are rhomboidal, the shape characteristic of most temnospondyls. Huxley's specimen, on the other hand, has a stemmed interclavicle, which suggests anthracosaur rather than loxommatoid affinities.

Thus apart from the holotype only two specimens, both from the Gilmerton Ironstone, may be tentatively attributed to this species. The first, described as 'a fine labyrinthodont jaw of *Loxomma*' was exhibited at the Geological Society in 1904 (*Proc. Geol. Ass.* 1906), by W. F. Gwinnell. The best of Gwinnell's collection was bought in 1920-1 by J. W. Gregory of Glasgow (Sherborn 1940), but since it has been impossible to locate this particular specimen the identification cannot be confirmed.

The second specimen B.M.(N.H.) R310 is an incomplete right jaw ramus (Panchen 1973, fig. 2, pl. 16, 1). It was attributed to the genus '*Macromerium*' (for *Macromerion* Fritsch 1889) on the nature of the teeth as '*Macromerium*' *scoticum* Lydekker 1890. *Macromerion* contains a number of unrelated Upper Carboniferous tetrapods (see Panchen 1970 under *Menonomenos*) and this specimen should certainly not be referred there. Romer (1947) and Panchen (1970) tentatively attributed this jaw to *Crassigyrynus scoticus* also from the Gilmerton Ironstone, but after further preparation of the two specimens Panchen (1973) now rejects this association, and favours attribution to *L. allmanni*. He compares the jaw with the present restoration of *Megalocephalus pachycephalus* (see below) and notes that they correspond in their general form, in the pattern of their dermal bones, the position of the lateral line, in the possession of teeth with keeled fore and aft margins and of a large parasymphysial tusk and an adjacent large tooth pair.

Panchen notes that the major differences of the specimen from *Megalocephalus* lies in the poor development of the normal loxommatid pit and ridge ornament over much of the dentary (though this varies between specimens of *Megalocephalus*) and also over known areas of the angular and surangular in the former, and in the smaller size of teeth in '*Macromerion*' and the recurved form of its parasymphysial tusk.

Although *Megalocephalus* is the only genus for which a loxommatid jaw can be reconstructed in detail, a complete lateral jaw surface is also known for *Baphetes lintonensis* and a virtually complete left ramus (R.S.M. 1967.201) from the Boroughlee Ironstone, may probably be referred to an indeterminate species of *Loxomma*. Although all show the same general pattern of dermal bones, the latter two differ from *Megalocephalus* in the same way as does the '*Macromerion*' jaw. The dentary of the Boroughlee jaw lacks the normal ornamentation and in *B. lintonensis* striations occur over the entire surface of the surangular, the upper half of the angular and over all but the symphyseal region of the dentary. This small specimen has teeth of similar proportion to those of '*Macromerion*' and the parasymphysial tusk is recurved in a similar fashion. Relatively small tusks in this region are to be expected in those genera which, in contrast to *Megalocephalus*, have no palatal fenestration for their reception. Thus since the '*Macromerion*' jaw is of loxommatid type and is of the correct size for the estimated skull length of *L. allmanni* I would endorse its attribution to this species.

LOXOMMA ACUTIRHINUS WATSON 1929

Specific diagnosis. Since the anterior part of the skull is not known for the other two species only the following distinction can be made. Loxommatids of the genus *Loxomma* in which the supratemporal extends around the otic notch on the dorsal surface only.

Description of material

Holotype. G.S. 27107. Skull, embedded in ironstone seen from the ventral surface and counterpart (G.S. 28314) of the anterior region of the palate. From Airdrie or 'Mushet's' Black Band Ironstone, Airdrie, Lanarkshire, Scotland. Upper Modiolaris zone, Westphalian B (Panchen & Walker 1961).

Watson's original description of this species (1929, pp. 237–8, figs. 14 and 15) was based solely on the holotype skull. Discovery, in the British Museum collection, of a second skull B.M.(N.H.) 37955 now makes a more complete morphological account possible. This specimen is also from Airdrie, but no horizon was recorded when it was purchased in 1863. Matrix from the skull was sent to Dr A. H. V. Smith of the National Coal Board and on the basis of the spore assemblage he dated it as Upper Modiolaris or Lower Similis–Pulchra zone. Since the Airdrie Black Band Ironstone is situated near the top of the Modiolaris zone (Panchen & Walker 1961), it is likely that B.M.(N.H.) 37955 is from the holotype horizon and locality.

Dermal skull roof

The holotype skull (figure 2*a*) together with the counterpart of its anterior palate (figure 2*b*) give an outline for dorsal reconstruction (figure 3*a*). The suture pattern is largely that of the ventral surface, since the dorsal surface of B.M.(N.H.) 37955 is badly eroded. Only the areas of ornament that are preserved in this specimen are included in the reconstruction. Owing to the manner of preservation of both skull specimens, there is no evidence of the lateral line system for this species. Skull shape is roughly that of an equilateral triangle, the width measured at the back of the premaxillae being only a third of that across the quadratrojugals. The orbits lie near the midregion of the skull, the antero-medial orbital border being demarcated by a lateral process of the prefrontal bone. As in other loxommatids the orbits proper appear to be approximately circular in outline, and compared to normal rhachitomes such as *Edops* or *Eryops*, lie relatively close to the midline of the skull. The orbit is extended anteriorly by the peculiar loxommatid antorbital fenestra, which in this genus is of about the same size as the orbit proper. The lateral wall of the antorbital fenestra is solid, since the lachrymal and jugal unite with dorsal buttresses from the underlying palatal elements, to form a continuous smooth-sided wall parallel with the skull margin.

The external nares are subcircular in outline and lie near the margin of the skull, the position thought to be primitive for tetrapods (Säve-Söderbergh 1932; Westoll 1943; Panchen 1967). They lie well behind the tip of the snout since the premaxillae are relatively elongated, as in *Megalcephalus* but in contrast to *Baphetes*. Although it was presumably present, the septo-maxillary bone is not apparent from the ventral surface of the type skull and thus the exact nature of the narial region is not known.

From the shape of the anterior part of the nasals, it seems likely that internasal ossicles were present in the midline, as in other loxommatid genera. The frontal bones appear to be more splint-like than in *L. allmanni*, but since the holotype of the latter is asymmetrical this feature is not included in the specific diagnosis. As in *L. allmanni* the parietals are raised around the pineal foramen in the topotype skull and it seems probable that the pineal was above the general level of the skull table.

The major difference apparent between this species and *L. allmanni* is in the otic notch. The supratemporal extends around the anterior border of the otic notch on the dorsal surface, while an extension of the squamosal underlies it and sutures with the tabular ventrally.

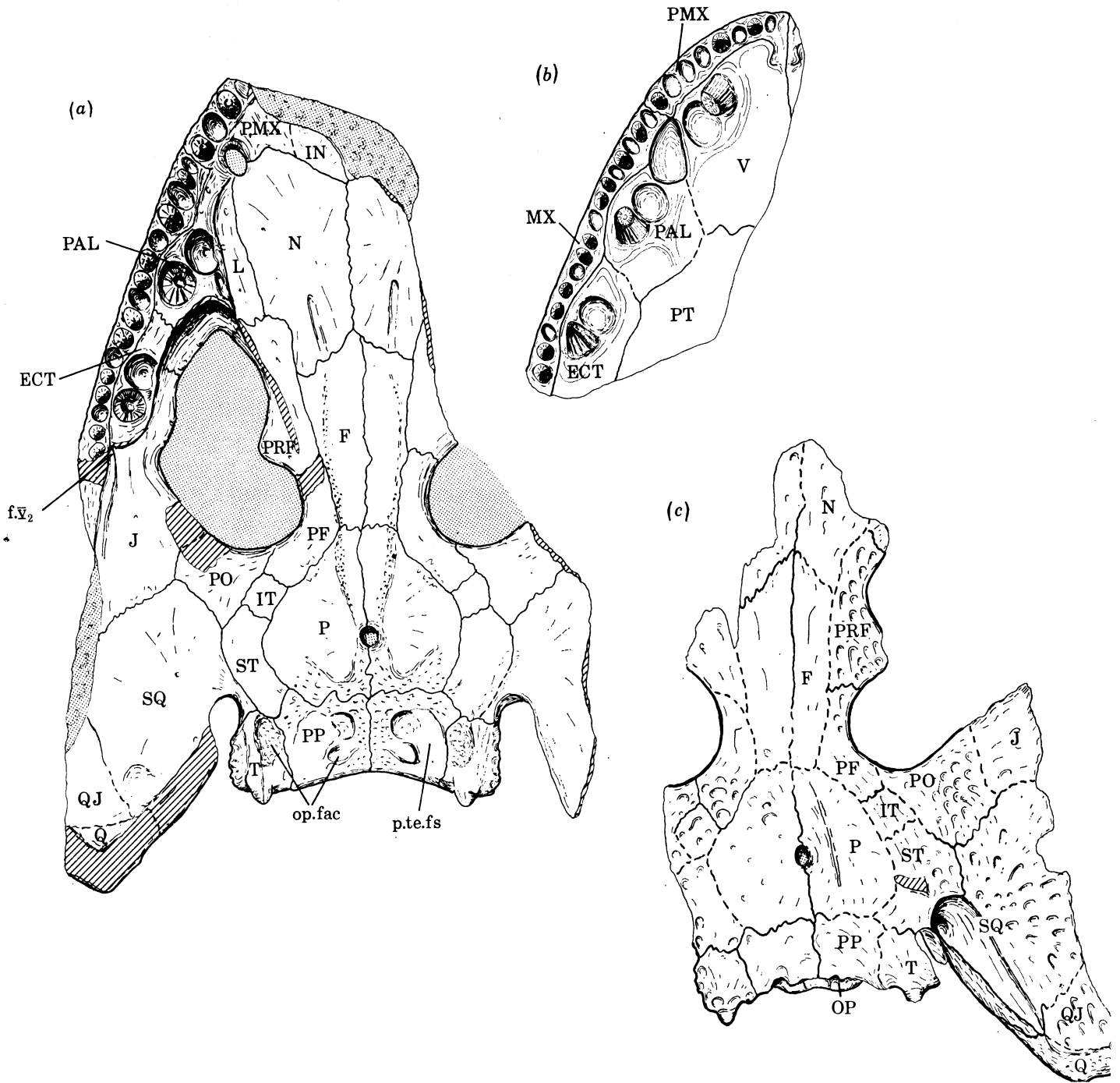


FIGURE 2. *Loxomma acutirhinus* Watson: (a) ventral surface of holotype skull roof, (b) cast of counterpart of anterior palate of holotype, (c) B.M.(N.H.) 37955 in dorsal view. Half natural size. Matrix stipple, broken bone hatched.

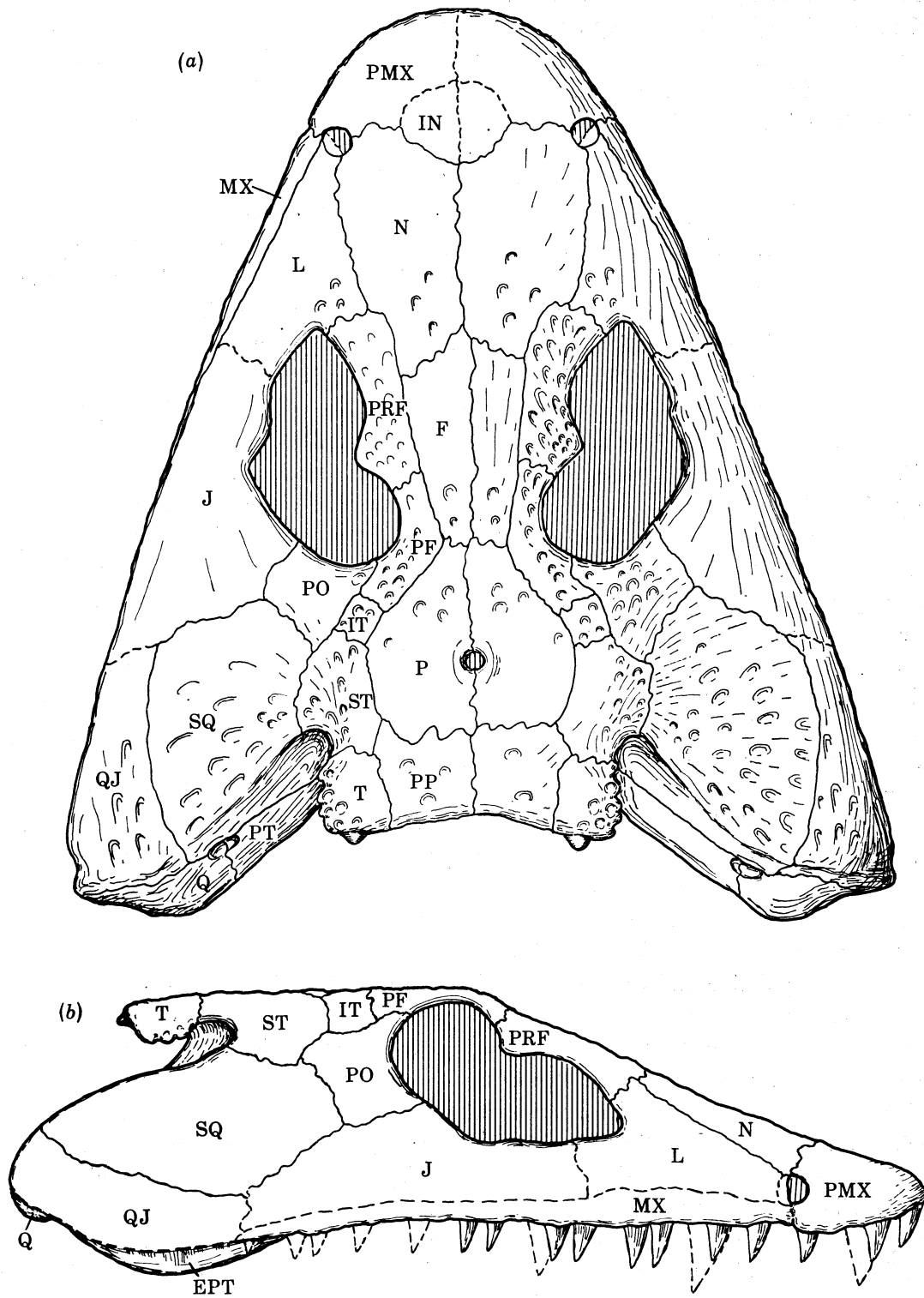


FIGURE 3. *Loxomma acutirhinus* Watson, composite restoration of the skull: (a) dorsal, (b) lateral view. Half natural size.

The quadrate lies, as in most primitive labyrinthodonts, well behind the level of the occiput and the cheek region is relatively long and deep. Both specimens have suffered considerable compression, but in life *L. acutirhinus* probably had a relatively high, rounded skull. An attempt has been made to correct the curvature in the lateral reconstruction (figure 3*b*). The ventral surface of the dermal skull roof is discussed below in relation to the braincase.

Palate and palatoquadrate

In this species the palate is only known in part, but indications are that it was of the primitive temnospondyl pattern. The alveolar surface of part of the premaxilla and maxilla are preserved in the holotype skull, together with the area of palatine and ectopterygoid around the tusk pairs, since this latter region is firmly connected to a ventrally projecting shelf from the jugal and lachrymal of the skull roof, forming a solid lateral wall to the antorbital vacuity. Further information on the structure of the anterior part of the palate was gained from positive latex casts, taken from the counterpart block of the anterior snout (figure 2*b*). This specimen also bears an impression of the choana, which is ovoid in shape with a maximum length of 20 mm. In B.M.(N.H.) 37955 all the palatal elements are missing apart from the quadrate ramus of the pterygoid and broken remnants of this element in the region of the conical recess (figure 4*a*). However, the palatal ramus of the epipterygoid remains intact on the right side of the skull and confirms that the palate was of the simple closed type, lacking interpterygoid vacuities.

Each premaxilla bears eight teeth. These are relatively small near the median suture, but increase in size as the alveolar shelf broadens posteriorly. Mesially the palatal surface of the premaxillae thickens to form a pair of stout rounded midline buttresses, as in *Megalocephalus* and *Baphetes*. Since there is no anterior palatal fenestra, the premaxilla sutures with the vomer along the whole of its length. This solid anterior palate presumably means that parasymphysial tusks of the dentary were not unduly elongate.

The maxilla is incomplete in the type skull, there being 16 teeth (including replacement pits) up to the point behind the level of the last ectopterygoid tusk, where the bone is broken. The maxillary teeth form a graded series, there being a gradual decrease in alveolar size along the length of the bone. It is estimated that possibly 10–12 teeth would lie posterior to those preserved, taking into account the maximum length probable for the maxilla. It is unlikely therefore that its tooth count would exceed 30.

The vomer, palatine and ectopterygoid all have a single tusk and replacement pit borne together on a raised boss, but those of the ectopterygoid have a somewhat smaller basal diameter than those on the other two elements. Apart from the posterior part of the ectopterygoid, the extent of all three bones can be determined from the holotype counterpart slab.

The anterior region of the palatal ramus of the pterygoid is also preserved in the counterpart specimen. A shagreen of denticles is apparent over its general surface. The quadrate ramus of the pterygoid is preserved in the other skull (B.M.(N.H.) 37955). It passes back along the mesial wall of the subtemporal fossa to suture with the quadrate and is overlapped dorsally by the squamosal flange. The pterygoid also forms the lip of the conical recess of the basal articulation. This structure has been distorted and pushed backwards over the basipterygoid process in B.M.(N.H.) 37955 (figure 4*a*). In this skull the palatal ramus of the pterygoid has sheared off and is completely missing, so that part of the epipterygoid is revealed. Thus the palatal ramus of the epipterygoid was ossified as a separate sheet of bone lying dorsal to the pterygoid, in the region anterior to the conical recess. The extent of this ossification (figure 4*a*) corresponds closely

to that figured by Panchen (1964, fig. 16) in '*Eogyrinus*' (in error for *Pholiderpeton*, Panchen 1970); but differs from *Megalocephalus*, where pterygoid and epipterygoid largely co-ossify around and in front of the basal articulation (figure 10*b*). The extent to which the epipterygoid forms the conical recess is not clear, due to poor preservation of this region. Just in front of the basal articulation the mesial epipterygoid slopes up towards the skull roof, this strut probably representing the columella cranii. Anteriorly the ramus is a horizontal sheet of bone, which abuts against the side wall of the braincase, effectively 'closing' the palate. The quadrate ramus of the epipterygoid is not known.

Braincase and parasphenoid

The ventral surface of B.M.(N.H.) 37955 was cleaned of matrix to expose a relatively well-preserved braincase (figure 4*a*). The bone surface is slightly eroded, particularly in the posterior region. Here some of the elements have sustained damage, presumably as the occipital arch was squeezed out (figure 4*b*). However, apart from the occipital condyle and the posterior margin of the parasphenoid, the specimen is complete and is the only loxommatid for which the ethmo-sphenoid portion of the neurocranium is known.

It is fortunate that the pterygoid complex is missing from the left side of the skull, thus enabling examination of the lateral wall of the otic region, for although the skull has undergone slight dorso-ventral compression the major foramina for the cranial nerves are still apparent. The post-temporal fossa has, however, been almost closed up and the parasphenoid has been pushed forward and slightly to one side in the otic region. The latter has resulted in a flattening of the basiptyergoid processes and has opened up the left otic capsule, exposing part of the course of the semicircular canals in its roof. This slight forward shift of the posterior parasphenoid has also resulted in a distortion of the midregion of the cultriform process, deflecting it laterally.

This new specimen together with the excellent braincase impression on the holotype skull roof make it possible to reconstruct a loxommatid braincase for the first time (figure 4*c-e*). The occipital arch is not known for *Loxomma* but the limited information available (figure 4*b*) suggests that it is in all respects similar to that of other loxommatids. It has been restored from that of *Megalocephalus* and restoration in occipital aspect will be discussed in detail only for that genus.

From B.M.(N.H.) 37955 it is obvious that the whole of the loxommatid braincase was heavily ossified and the extensive areas of attachment to the dermal roofing bones apparent in the holotype skull (figure 2*a*) indicate that the structure was more or less completely roofed in cartilage bone as in other primitive labyrinthodonts. A further feature of the braincase is its tropibasic condition, a feature common to primitive rhachitomes in contrast with the persistently high sphenethmoid of anthracosaurs.

The median parasphenoid, although dermal in origin, is considered with the braincase since it forms an integral part of its structure. It unites sphenethmoid and otic portions, as is the normal condition for labyrinthodonts apart from *Ichthyostega*. Details of its construction will be considered below in association with the relevant areas of neurocranium.

As noted above the occipital arch has been lost from the neurocranium. However, the opisthotic bears a pair of facets for columns of the exoccipital and these alone indicate a structure more primitive than that hitherto described for any temnospondyl.

The very limited extent to which the exoccipital enters into construction of the braincase certainly represents a primitive condition. It is essentially that of the cartilaginous embryonic

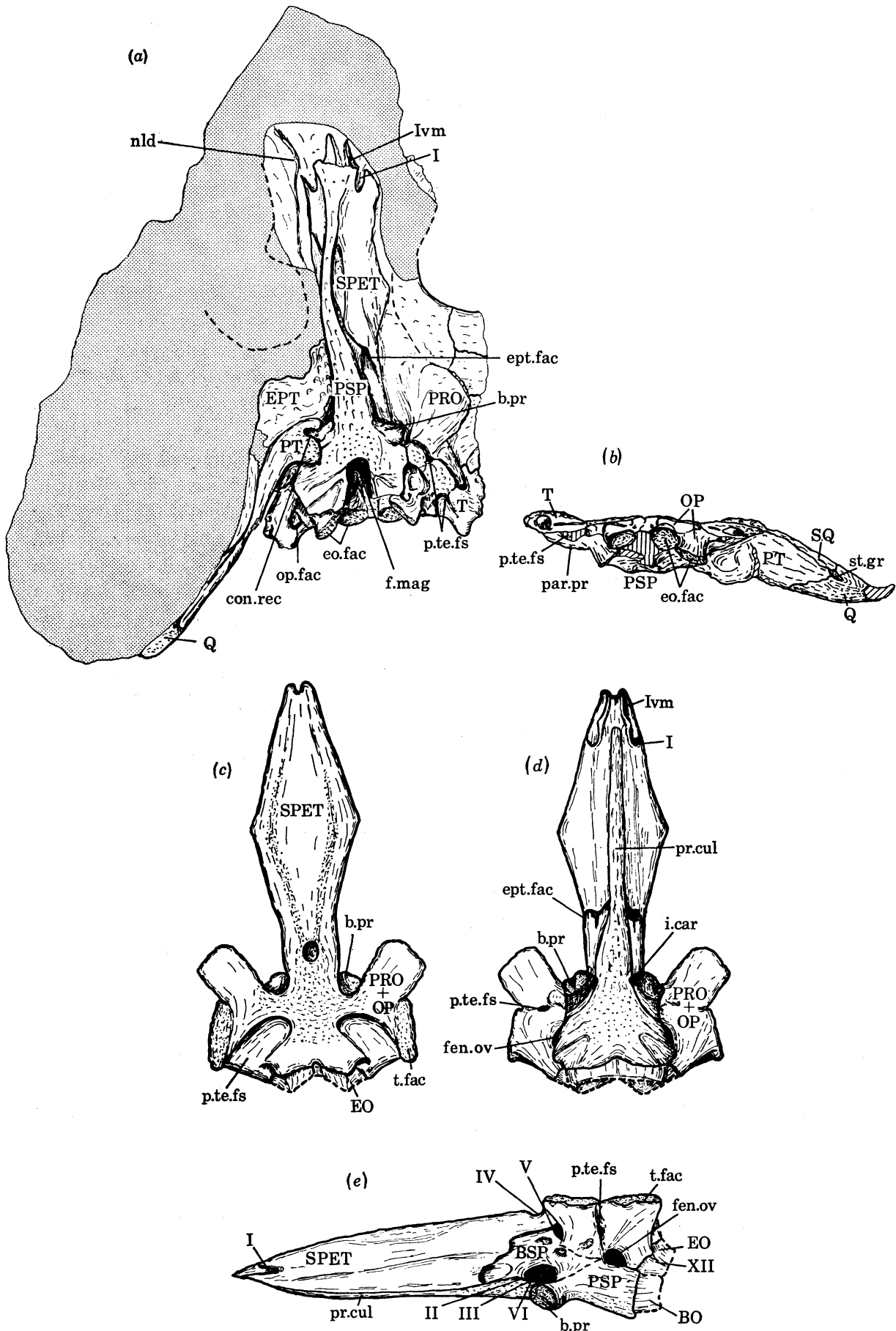


FIGURE 4. *Loxomma acutirhinus* Watson, braincase, half natural size: (a, b) B.M.(N.H.) 37955 as preserved, ventral and occipital views; (c-e) Composite restoration, dorsal, ventral and left lateral.

occipital arch, and is only weakly attached into the back of the skull, the areas of contact always being with cartilage finished surfaces, hence loss of the structure in all loxommatids apart from two specimens of *Megalocephalus*. The 'reptiliomorph' stock remain primitive in this respect, but among temnospondyls the exoccipitals gradually come to invade areas formerly ossified by the opisthotics and finally become an integral part of braincase construction. The occipital arch is thus firmly incorporated into the back of the skull. Even in *Edops*, the exoccipitals extend upwards to reach the postparietals and continue forwards under the dermal roof to merge into the upper surface to the otic region of the braincase, a considerable advance on the condition found in *Loxomma*.

It is likely that cranial nerves IX, X and XI emerged between the exoccipital facets of the opisthotic (see *Megalocephalus*). The opisthotic extends laterally as the paroccipital process, forming the lower border of the post-temporal fossa and contacts a facet on the tabular. A median suture of the paired opisthotics is not apparent in this species, but is extremely prominent in the holotype of *Baphetes kirkbyi* (figure 19a, b) in the region of the synotic tectum, indicating that in that loxommatid species there was no supraoccipital ossification (see discussion of occipital aspect for *Megalocephalus*).

The otic capsule is apparent on the left side of the topotype. Its postero-lateral wall is formed from the curved anterior face of the more lateral of the facets for the exoccipital. The outer surface of the facet extends antero-laterally as a smooth process, its dorsal border forming the rim of the post-temporal fossa, and its ventral border the upper margin of the fenestra ovalis. The latter is a large perforation in the lateral wall of the otic capsule, which has been opened up in the topotype due to the forward shift and slight erosion of the parasphenoid. This dermal element formed the floor of the capsule and the lower rim of the fenestra ovalis.

The post-temporal fossa extends above, and is floored by, the otic capsule as does the cross-apterygian fossa bridgei, with which it is homologous. Its dimensions are apparent from an impression on the holotype skull roof. The fossa extends through and perforates the otic region, anterior and somewhat dorsal to the fenestra ovalis. The vena capitis dorsalis is believed to have entered the fossa through this opening. A groove which passes laterally from this foramen may indicate part of the boundary between opisthotic and pro-otic ossifications. The more postero-medial continuation of this line of suture is not apparent, but where it is known for other labyrinthodonts extends to the fenestra ovalis so that both these ossifications enter into its margin. Attachment surfaces for the otic region of the braincase between the post-temporal fossae are apparent on the postparietals of the holotype skull.

The pro-otic has lateral wings extending anteriorly and attaching to the supratemporal and parietal bones. The supratemporal is grooved for reception of the lateral margin of the pro-otic, the area being an extension of the normal otic facet on the tabular. This peculiar winged otic region appears to be a characteristic of all loxommatids.

Ventrally the otic region of the braincase is sheathed by the expanded posterior section of the parasphenoid. As was noted earlier, this element is somewhat eroded in the topotype skull, particularly in the midregion and along its left posterior margin, but is reasonably well-preserved on the right side of the specimen. A prominent feature of the parasphenoid in the otic region are two V-shaped depressions, each defined by a pair of ridges, which run postero-laterally towards the margin of the bone. It is assumed that each sulcus and bounding ridges represent an area of attachment for neck musculature.

The parasphenoid extends around the basisphenoid core to sheath the basiptyergoid process

postero-mesially. This is somewhat distorted due to post-mortem compression, and details of the articular faces can be described only for the genus *Megalocephalus* (described later). The foramen for the internal carotid artery perforates what is assumed to be the boundary between basisphenoid and parasphenoid. In front of the foramen the latter extends forward as the slender processus cultriformis.

The basisphenoid is exposed in lateral aspect in the topotype skull. It extends antero-dorsally from a point somewhat behind the basiptyergoid process and forms the wall of the latero-sphenoid region. The basisphenoid is inset relative to the sphenethmoid and this inset area presumably formed the contact-surface for the eipterygoid processes dorsal to the basiptyergoid process, one of which lies in the pro-otic region. These facets have laterally directed articular faces.

Above the basal process, the basisphenoid forms the dorsal rim of a large foramen, which is floored by the parasphenoid (figure 4 *e*). The whole of this general area forms a deep concavity perforated by the foramen. Where such a structure has been described (Sawin 1941; Säve-Söderbergh 1944; Panchen 1959, 1964) the concavity is assumed to be the site of origin for part of the rectus eye musculature. It is therefore probable that the third (oculomotor) and sixth (abducens) cranial nerves, which enervate the rectus muscles, emerged through the foramen. Since there is no separate perforation for the optic nerve it is assumed, as in *Palaeoherpeton* (Panchen 1964), that this too emerged from the same foramen.

A second foramen is situated above the concavity. It is floored by the basisphenoid but the sphenethmoid and pro-otic form its upper and posterior borders. This is assumed to be the pro-otic foramen, for rami of the fifth cranial nerve. Another foramen, presumed to be for the fourth cranial nerve is usually described in this region. There is no indication of this in *Loxomma*, but in a specimen of *Baphetes* (figure 20) there is evidence that this nerve left the braincase slightly anterior to the pro-otic foramen and in a somewhat more dorsal position, between the sphenethmoid and the skull roof.

The sphenethmoid has a broad area of attachment with the skull roof (figure 2 *a*) and fans out slightly at about the level of the front of the postfrontal bone. The ossification is roughly triangular in cross-section, the narrow lower margin being ensheathed by the cultriform process (figure 4 *d*). Anteriorly the sphenethmoid extends to the level of the front of the antorbital vacuity. Dorsally it passes above the basisphenoid back to the level of the otic region. A pair of large canals emerge at the front of the sphenethmoid and were undoubtedly for the first cranial nerves. It seems probable from the size and shape of the aperture that the vomero-nasal nerve (Sawin 1941) ran forward along the curved mesial border of the structure, the main olfactory tract passing antero-laterally towards the nasal capsule (figure 4 *d*).

In *Edops* (Romer & Witter 1942) there is a further canal through the sphenethmoid slightly ventral to those for the olfactory nerves. It is thought that the profundus branch of nerve \bar{V} looped through this tunnel passing forward to unite with the superficial ophthalmic. In *Palaeoherpeton* (Panchen 1964 as '*Palaeogyrinus*') this course is marked by a deep groove. The specimen of the braincase of *Loxomma* shows no indication of the course of the profundus nerve and since the left side of the braincase is relatively undamaged it can be reasonably assumed that the profundus passed forward without piercing the lateral wall of the sphenethmoid.

LOXOMMA RANKINI SP. NOV.

Specific diagnosis. Loxommatids of the genus *Loxomma* in which the squamosal does not extend around the otic notch on either surface of the skull roof. Skull table comparatively short and broad, with reduced tabular and postparietal. Small pineal foramen flush with the surface of the skull table.

Description of material

Holotype. Hunterian Museum V 2023. Skull table, left cheek region and posterior half of right jaw ramus from the Drumgray Coal, Castlehill, near Carlisle, Lanarkshire, Scotland. Communis zone, Westphalian A.

Apart from the thin layer of coal shale between the skull roof and palatal bones, and that supporting the fragment of quadrate ramus of epityrgoid this fragmentary skull has been cleared of matrix on both sides (figure 5).

It resembles specimens of *Megalocephalus* (see below) in the diminutive nature of its dermal ornament and in the proportions of the bones of the skull table, with its relatively short tabular and postparietal. Also the pineal foramen is small and flush with the general surface of the parietals. The specimen is, however, obviously not *Megalocephalus*, since a small intertemporal bone is present.

Among loxommatids an intertemporal ossification is a feature of both *Loxomma* and *Baphetes*. These two genera can be distinguished mainly from the nature of the snout region, which is unfortunately missing in this skull. Reference of the skull to the former genus has thus been mainly on stratigraphical grounds. The earliest known specimen of *Baphetes* is from the Modiolaris Zone, Westphalian B, whereas this is from a horizon in the Communis Zone, which is Westphalian A. Further, the skull shows a slight advance over that of *Baphetes* in the possession of a relatively short skull table with a very small intertemporal bone. The size of the latter element allows a relatively long sutural contact of postorbital and prefrontal, as in *Loxomma allmanni*, so that the postorbital lacks the long finger-like process that seems to characterize *Baphetes*.

The specimen has thus been referred to a new species of *Loxomma*, as *L. rankini*, after Dr D. R. Rankin who collected it. Specific distinction seems justified since the skull differs in a number of features from the two species of *Loxomma* previously described (see diagnosis) and lies between them stratigraphically. The diminutive scale of the ornament is not included in the diagnosis since it may be a size-related factor.

The specimen, although of taxonomic significance, adds little information to knowledge of loxommatid skull morphology. During preservation the skull has undergone considerable compression and an oblique force has shifted the braincase and palatal structures anterolaterally. In addition, this has caused the right pterygoid ramus to shatter and fold, exposing the broken surface of the extensive epiptyrgoid ossification behind the conical recess. The posterior part of the braincase has been sheared off, presumably when the specimen was collected, and the compressed nature of the remainder of the otic region, partially covered by palate, has obscured the critical areas of the braincase.

The pattern of bones in the lower jaw is essentially that figured for other loxommatids, although the relationship of elements around the articular region apparently varies slightly from the condition described below for *Megalocephalus*. The discrepancy lies in the structure of

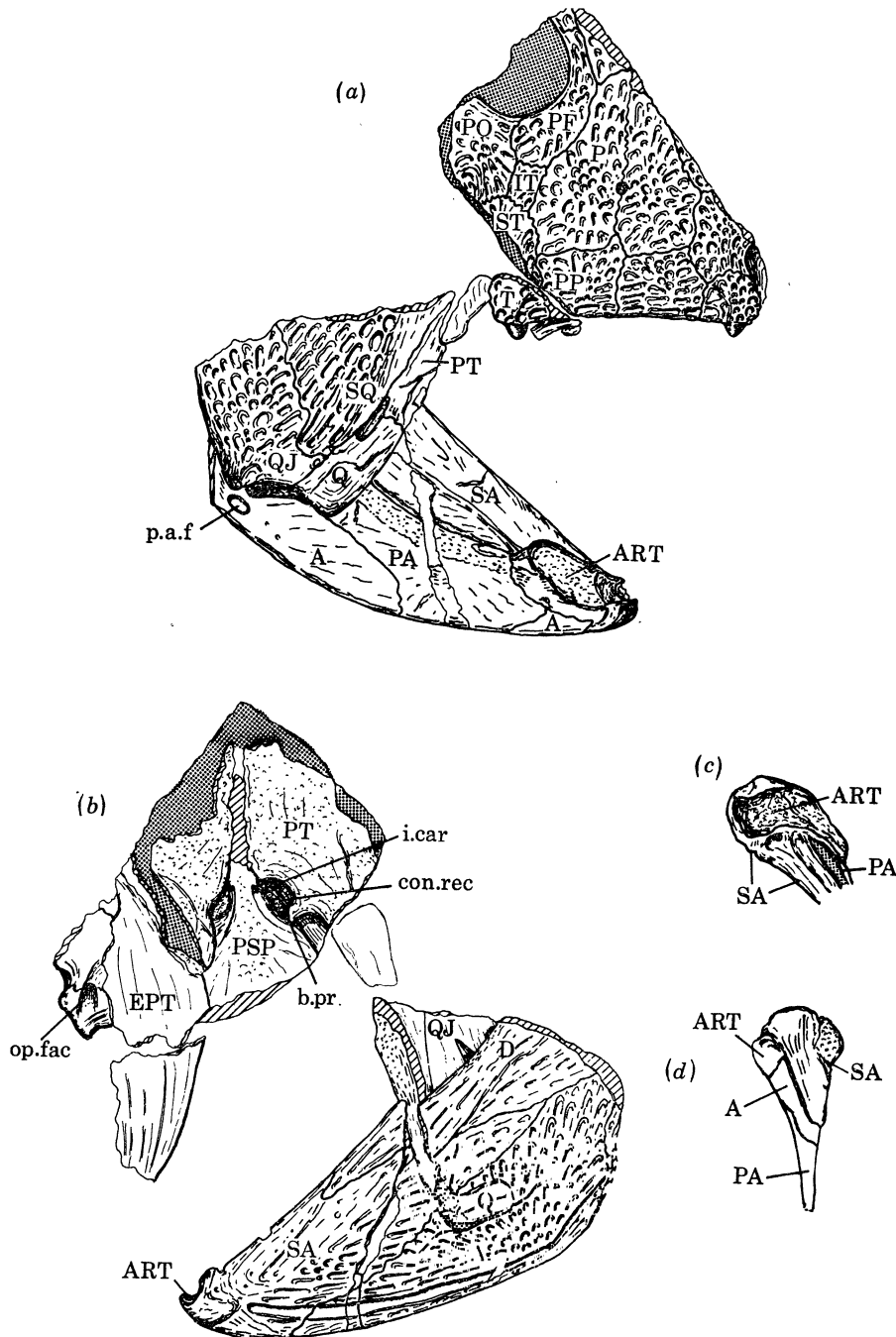


FIGURE 5. *Loxomma rankini* sp.nov., holotype skull. Two-thirds natural size: (a) dorsal skull roof and lower jaw in mesial view, (b) palate and lower jaw in lateral view, (c) articular region in dorsal view, (d) articular region in posterior view.

the angular bone which here has a small additional exposure on the mesial surface. This takes the form of an attenuated process which extends from the posterior region of the lateral exposure of the angular round onto the mesial surface, where it separates pre-articular and surangular ossifications (figure 8*a, d*). A similar condition occurs in *Eryops* (Sawin 1941).

The lower jaw is broken just in front of the posterior angular foramen, a structure not generally developed in other labyrinthodonts, but apparently a feature of loxommatids.

INCERTAE SEDIS

A further specimen may possibly be referred to the genus *Loxomma*, although not necessarily to any of the above species. It consists of a left lower jaw ramus which is undoubtedly temnospondyl and has a suture pattern which corresponds to that known for loxommatids.

The jaw bone (R.S.M. 1967 201), which is complete apart from its extreme anterior end, is from the Boroughlee Ironstone of Loanhead, Midlothian, Scotland. This horizon lies at the base of the Namurian, in the Limestone Coal Group. *Spathicephalus mirus* (Loxommatoidea, Spathicepalidae) occurs in the same stratum and part of a lower jaw is known in this species. This is shallow with pustulate ornament and has spatulate teeth. The present jaw ramus has the reticulate ornament and lanceolate teeth characteristic of the Loxommatidae.

Baphetes and *Megalocephalus*, are not known from strata below the Coal Measures and in any case the specimen cannot be referred to *M. pachycephalus* since it exhibits no peaking of the dentary teeth. Since it is of primitive loxommatid structure and its occurrence is relatively early, the jaw specimen may be tentatively referred to the genus *Loxomma*, but is specifically indeterminate.

GENUS *MEGALOCEPHALUS* BARKAS

Generic diagnosis. Loxommatids with a high, triangular skull. Known midline length up to 350 mm. Pre-orbital region approximately two-thirds midline length. Antorbital vacuity at least twice as long as orbit. Premaxilla long, bearing eight or nine teeth. Lachrymal separated from nostril by naso-maxillary suture. Skull table comparatively short. Intertemporal bone absent, with corresponding area occupied mainly by the supratemporal. Maxilla contacts quadratojugal, excluding jugal from skull margin. Palate with anterior fenestra for parasymphysial dentary tusks.

MEGALOCEPHALUS PACHYCEPHALUS (BARKAS 1873)

Comb. Lehman (1955, p. 73)

Specific diagnosis. Loxommatids of the genus *Megalocephalus* with a long cheek region, the quadrates lying well behind the level of the occiput. Tabulars relatively square with a well-developed posterior boss. Three distinct peaks in tooth size along the dentary. (Further diagnosis is not possible due to the paucity and relatively smaller size of all known American specimens of the genus).

Distribution. Coal Measures (Westphalian A-C) of Great Britain and Eire.

Megalocephalus is the first available generic name for what appears to be the most common genus of labyrinthodont amphibian from the British Carboniferous. There are no records from Viséan or Namurian localities, but from their first appearance in the Communis zone, Westphalian A, specimens of this genus occur until the Phillipsii zone at the top of Westphalian C. Specimens of *Megalocephalus* have been collected at Swanwick (Derbyshire), Coalbrookdale (Shropshire), Newsham (Northumberland), Fenton, Longton and Shelton (North Staffordshire) in England, from Jarrow (Co. Kilkenny) in Eire, and in Scotland from Pirnie (Fifeshire) and various horizons around Airdrie (Lanarkshire).

The greatest number of specimens from any one site come from the Black Shale, overlying the Low Main Seam at Newsham. The first of these was believed by Kirkby & Atthey (1864)

to be a 'fragment of the mandibular bone of *Rhizodus lanciformis* Newberry'. The specimen that they figure is in fact a fragment of dermal roofing bone and palate of *Megalocephalus*. Later (1868) Hancock & Atthey comment on the 'reptilian' nature of this species. *Rhizodus lanciformis* is evidently in error for *Rhizodus lancifer* Newberry (1856), the type of which is a fragmentary tooth believed by Romer (1963) to be from an anthracosaur ('*Anthracosaurus lancifer*'). '*Lanciformis*' therefore was a lapsus calami, and is not available as a specific name for *Megalocephalus*.

In 1868 the first labyrinthodont skull tables were found at Newsham and named *Pteroplax cornuta* by Hancock & Atthey. Found at the same time and therefore attributed to this new species were premaxillary bones of *Megalocephalus* (Hancock & Atthey 1868 pl. 1, fig. 3) and thus the tooth structure and 'honeycomb' dermal ornament characteristic of loxommatids were listed as diagnostic of *Pteroplax*. Therefore, when in 1869 two loxommatid skulls from the 'Mushet' Blackband Ironstone at Quarter came into the possession of Mr James Thomson of Glasgow, they were attributed to the genus *Pteroplax*, but as a new species *P. brevicornis* Thomson & Young 1869. The specific name refers to the size of the small loxommatid tabular boss, which is quite distinct from the long tabular horn of *P. cornuta* and other anthracosaurs.

Previous to the discovery of *Pteroplax* in 1868 the only large labyrinthodont amphibians described from the British Coal Measures were *Anthracosaurus russelli* Huxley 1863 and *Loxomma allmanni* Huxley 1862, and it is not surprising that *Megalocephalus* specimens have been wrongly attributed to both these forms. As only the palate was exposed in the former, and the posterior part of a skull roof displayed from the ventral surface of the latter, differences in ornament and arrangement of bones between anthracosaurs and loxommatids were not apparent. In 1869 an anterior portion of a skull of *Eogyrinus attheyi* Watson 1926 was discovered at Newsham and described as *Anthracosaurus russelli* by Hancock & Atthey (1869). They also attribute to this species a specimen described earlier that year by Barkas (1869, p. 419) as a crocodile 'malar'. This specimen is figured by Barkas in 1873 (fig. 187) and is clearly part of a crushed *Megalocephalus* skull.

In 1870 the first almost complete *Megalocephalus* skull was found at Newsham. This specimen (H.M. G15. 23, figure 10) was in an excellent state of preservation, although missing the snout region, and clearly shows the typical loxommatid orbits. Because of this feature Hancock & Atthey believed it to be a specimen of *Loxomma allmanni* Huxley and they also referred Thomson's *Pteroplax brevicornis* specimens to this form.

In 1871 a complete *Megalocephalus* skull (H.M. G15. 21,) with parts of two lower jaw rami (H.M. G15. 39, H.M. G15. 46) probably from the same individual, were obtained by Atthey from the Low Main Seam (Hancock & Atthey 1871, p. 73). In 1875 Embleton and Atthey gave a very detailed account of this specimen, with excellent figures by Dinning. The following year Atthey described a complete *Eogyrinus* skull (as *A. russelli*), so that differences between these two common Coal Measure labyrinthodonts were now apparent, and from this time until Watson re-examined Carboniferous amphibian material in the 1920s, most recognizable loxommatid remains were referred to as *Loxomma allmanni*.

However, some confusion still existed in the 1870s, notably in a book by Barkas (1873) in which a large skull from Newsham (H.M. G15. 22, figure 6, plate 1) was described and figured (figs 183, 184, 185) as *Orthosaurus pachycephalus* Barkas gen. et sp.nov. While Barkas noticed similarities between this specimen and those normally attributed to *Loxomma*, he believed the pineal foramen to be absent in *Orthosaurus*, and therefore classifies it as a 'true reptile' rather than a labyrinthodont. Another specimen, a large skull minus the snout (B.M.(N.H.) R3417),



FIGURE 6. *Megalocephalus pachycephalus* (Barkas), holotype skull in dorsal view. Half natural size.

(Facing p. 46)

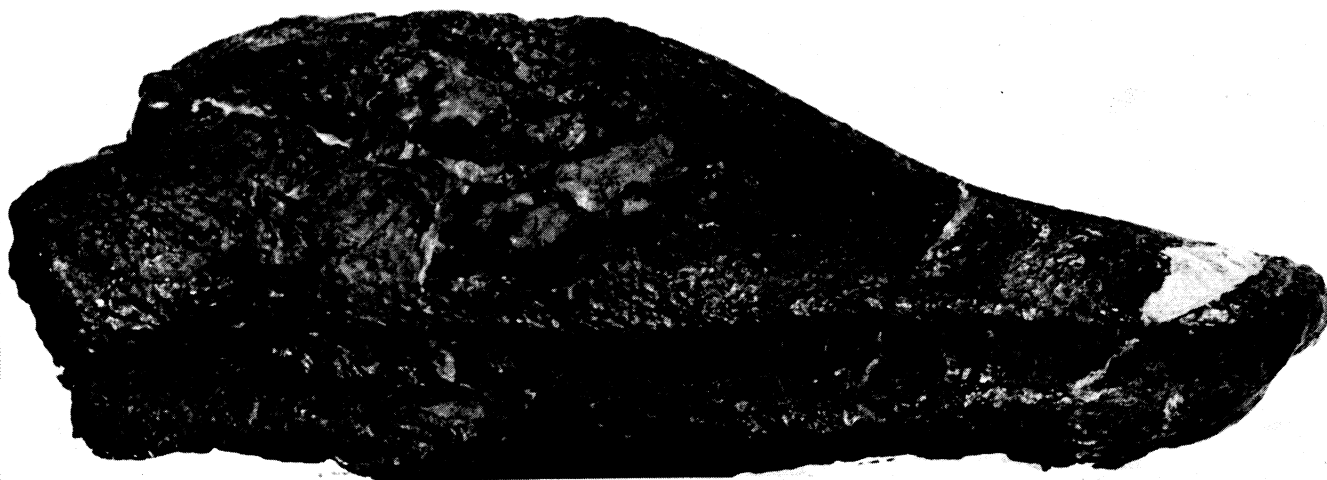


FIGURE 7. *Megalocephalus pachycephalus* (Barkas), Coalbrookdale skull.
B.M.(N.H.) R585 in right lateral view. Half natural size.

he described as *Megalocephalus macromma* Barkas (1873, fig. 90), a reptile which he believed differed from *Orthosaurus* in being a short-snouted form.

Most of the British *Megalocephalus* material was collected during the latter part of the nineteenth century. One of the best skulls (B.M.(N.H.) R585, figure 7, plate 2) which is preserved relatively uncrushed in an ironstone matrix, was found by Mr George Maw near Coalbrookdale, in Shropshire. This specimen was first figured by Miall in 1873 as *Loxomma*, and is the main basis for skull shape in later reconstructions.

In 1926 Watson, as part of his Croonian Lecture on *The Evolution and Origin of the Amphibia* gave a detailed account of skull structure of *Megalocephalus*, which as he points out is a form allied to, but distinct from *Loxomma allmanni*. Watson went back to the earliest certain name of this animal, which is *Orthosaurus pachycephalus* Barkas 1873).

Unfortunately as Kuhn pointed out in 1933 (p. 37), *Orthosaurus* is preoccupied, and he proposed *Orthosauriscus* to replace it. The name *Orthosauriscus* was used for this loxommatid during the following decade by a number of authors, most notably Säve-Söderbergh, Westoll and Kuhn, but Romer in his *Review of the Labyrinthodontia* (1947, p. 98) goes back to the alternative name of *Megalocephalus* Barkas 1873, which had been overlooked by Kuhn. Romer derives the first available specific name from '*Pteroplax*' *brevicornis* Thomson & Young 1870.

The collection of Mr James Thomson was presented to Kilmarnock Museum, and virtually all the amphibian material was destroyed, when the Museum suffered a fire in 1909 (Dunlop 1910, p. 60). Thomson's specimens had never been figured or adequately described, and although undoubtedly loxommatid the specific status of this material is uncertain. No material is now in existence that is certainly from Thomson's type locality. Thus since the specimens have been destroyed without a diagnostic account of the species '*Pteroplax*' *brevicornis*, it is therefore a nomen dubium (Simpson 1945). This being the case it is proposed to limit the specific name *Megalocephalus brevicornis* to refer to the specimens mentioned by Thomson and Young. The next available specific name *Megalocephalus pachycephalus* (Barkas 1873) has been taken for all other British material pertaining to this genus.

Description of material

Specimens from the Hancock Museum used by Watson (1926) in his description of this species were given a reference number preceded by the initials DMSW, but are also registered in the museum's collections.

Holotype. H.M. G15.22 (DMSW 2) (figure 6, plate 1). Nearly complete skull figured by Barkas (1873, figs 183-185) as *Orthosaurus pachycephalus* gen. et sp.nov. From the Black Shale above the Low Main Seam, Newsham, Northumberland, England. L. Similis-Pulchra zone, Middle Coal Measures (Westphalian B) (Panchen & Walker 1961).

Other specimens attributed to this species. Since fragments of this species are comparatively abundant only those specimens used in the description of the skull are listed below. The horizons at which they occur are arranged stratigraphically. A complete list is given elsewhere (Tilley (Beaumont) 1971).

From Jarrow Colliery, Castlecomer, Co. Kilkenny, Eire. Leinster Coalfield. L. Communis zone, Lower Coal Measures (Westphalian A) (Eagar 1961):

I.N.M. 187. Laterally compressed skull with lower jaws. Infilled natural cast.

B.M.(N.H.) R8465. Juvenile skull, 40 mm in length.

From Blackshale or Silkstone seam, Swanwick, Derbyshire, England. M. Communis zone, Lower Coal Measures (Westphalian A):

K.C. L1. Right side of skull table and cheek region, overlain by part of lower jaw ramus.

K.C. L2. Orbital and interorbital region, overlain by dentary.

From Blue Flats Ironstone, Coalbrookdale, Shropshire, England. L. Modiolaris zone, Middle Coal Measures (Westphalian B):

B.M.(N.H.) R585 (figure 7, plate 2). Skull with lower jaws preserved in the round, figured by Miall (1874, pl. 2).

From Airdrie or 'Mushet's' Blackband Ironstone, Larkhall, Lanarkshire, Scotland. U. Modiolaris zone, Middle Coal Measures (Westphalian B):

H.G. V2016. Right jaw ramus.

From Low Main Seam, Newsham, Northumberland. L. Similis-Pulchra zone, Middle Coal Measures (Westphalian B):

H.M. G15.21 (DMSW 1). Skull figured by Embleton & Atthey (1874), pls. 1, 2).

H.M. G15.23 (DMSW 3). Skull lacking the snout region and occipital condyle. Braincase figured by Embleton & Atthey (1874, pl. 3, fig. 1).

R 3417. Posterior part of a large skull. Figured by Barkas (1873, fig. 184) as *M. macromma* type specimen.

H.M. G15.27 (DMSW 7). Right cheek region with epipterygoid figured by Watson (1912, pl. 1).

H.M. G15.29 (DMSW 9). Isolated basioccipital, associated with palatine and other skull fragments.

H.M. G15.30 (DMSW 10). Middle region of snout.

H.M. G15.32 (DMSW 12). Right palatine belonging to G15.23, showing posterior margin of choana and naso-lachrymal duct.

H.M. G15.33 (DMSW 13). Left vomer.

H.M. G15.34 (DMSW 14). Premaxilla, showing perforation for dentary tusk, figured by Hancock & Atthey (1886, fig. 3).

H.M. G15.35 (DMSW 15). Premaxilla, showing perforation for dentary tusk.

H.M. G15.49. Snout and right orbital region.

H.M. G15.39. (DMSW 19). Anterior region of left jaw ramus, figured by Embleton & Atthey (1874 pl. 3, fig. 3). Probably same individual as G15.21 and G15.46.

H.M. G15.40 (DMSW 20). Middle region of right jaw ramus.

H.M. G15.43 (DMSW 23). Middle region of right jaw ramus.

H.M. G15.46 (DMSW 26). Right jaw ramus, figured by Embleton & Atthey (1874, pl. 3, fig. 2).

From Palace Craig Ironstone, Carnbroe, Lanarkshire, Scotland. L. Similis-Pulchra zone, Middle Coal Measures (Westphalian B):

G.S. 28319, 28320. Snout and both jaw rami.

From Ash Ironstone, Longton, Staffordshire, England. U. Similis-Pulchra zone, Middle Coal Measures (Westphalian C):

B.M.(N.H.) R2370. Middle region of skull, uncrushed.

From Chalky Mine (= Golden Hill) Ironstone, Fenton, Staffordshire, England. L. Phillipsii zone, Middle Coal Measures (Westphalian C):

B.M.(N.H.) R2364. Skull table.

The relative abundance of material for this species allows the morphology of its skull to be described in more detail than is possible for any other loxommatid. Thus a full account of the structure of individual bones will be given for this species only.

Dermal skull roof

Most of the material upon which description is based has suffered post-mortem compression, but the natural contour of the skull is preserved in B.M.(N.H.) R585 from Coalbrookdale (figure 7, plate 2). It is high with a deep cheek region and viewed dorsally the triangular shape is apparent. Measurements taken across the premaxillae and the quadratojugals indicate an approximate 1:3 increase in cranial breadth between these two points.

Three other *Megalocephalus* skull specimens are virtually complete. These are a laterally compressed specimen from Jarrow (an infilled natural cast which shows no detailed structure) and two very well preserved, though extremely compressed skulls from Newsham, the larger of which is the holotype (figure 6, plate 1). Their midline length (front of premaxilla to back of postparietal) varies from 298 mm (H.M. G15.21) to 333 mm in the holotype (H.M. G 15.22).

The quadrate region, missing in B.M.(N.H.) R585, but known from a number of other specimens, extends as in most other primitive labyrinthodonts well behind and lateral to the occiput. The total skull length varies from 351 mm (H.M. G15.21) to 396 mm (H.M. G15.22) but dimensions of incomplete specimens, B.M.(N.H.) R3417 from Newsham and K.C. L1 and L2 from Swanwick in Derbyshire, are larger than those for the holotype skull.

In the undistorted skull, the ratio of estimated total length to maximum width is 1.56, and maximum height to maximum width is 0.47. The orbits lie well behind the midlength of the skull, and are directed antero-laterally. The antorbital fenestra is relatively larger than in any other genus, its length extending to more than twice that of the orbit.

In the region between the antorbital fenestrae, the frontal bones form a shallow depression between a pair of prominent ridges on the prefrontals. These ridges continue forwards along the middle of each nasal bone until they join the supra-orbital lateral lines, just postero-medial to the external nares. The relatively elongate premaxillae result in the nares lying further back from the tip of the snout than in other loxommatids.

The skull table is relatively small compared with that of *Loxomma* and *Baphetes*. It is horizontal in the skull, and is firmly fused to the cheek region, which slopes down almost vertically. The pineal foramen is a small circular opening of about 4 mm diameter, situated approximately two-thirds of the way down the midline suture between the parietal bones. It is flush with the skull table, and not raised on any sort of boss or prominence.

The reticulate ornament on the dermal bones of the skull roof is well preserved in most specimens of *Megalocephalus*. It tends to be on a smaller scale than that of other loxommatid genera, particularly in the region of the skull table. On the lateral margins of the premaxillae it is represented by tiny shallow pits on an almost smooth surface. This feature is in contrast to *Baphetes* which is very deeply pitted around the skull margin.

In *Megalocephalus* the principal region of elongation of dermal bones, characterized by

elongation of the ornament, is in the median antorbital region and particularly the frontal, prefrontal and nasal bones. Ornament on the cheek region, notably the jugal, squamosal and quadratojugal, is elongated laterally. The length of the snout, in this genus, is correlated with a relatively long tooth row compared with that of other loxommatids.

The lateral line canals appear as deep, flat-bottomed grooves on the surface of dermal bone elements. Their course has been somewhat amended from that of Watson's original restoration (1926). The suborbital canal is apparently a continuation of the main lateral line of the body. Its normal course in labyrinthodonts is forwards along the lateral margin of the skull table, traversing tabular and temporal elements. It then turns down over the postorbital and jugal to run forwards below the orbit, usually looping onto the lachrymal before passing along the maxilla to the narial region (Romer 1947). There is no trace of this canal on the posterior part of the skull in any *Megalocephalus* specimen. Watson (1926) figures it as beginning on the prefrontals between the antorbital fenestrae, which would be an extremely unusual condition, but a depressed, infilled crack in H.M. G15. 21 followed the course of the original restoration, which when cleared of matrix showed normal reticulate ornament. However, the suborbital canal shows very clearly on the right side of B.M.(N.H.) R585 where it is looped on the lachrymal as though a continuation of its normal course from the jugal. Anteriorly it loops down onto the maxilla and terminates near the postero-lateral border of the naris.

The supra-orbital canals are first apparent on the anterior part of the nasals from whence they can be followed forwards as deep grooves onto the premaxillae. They are connected by the ethmoid commissure, which runs laterally across the premaxillae. The supra-orbital canal and ethmoid commissure converge near the skull margin approximately 2 cm in front of the anterior border of the naris, so that there is no anastomosis between suborbital and supra-orbital canals in *Megalocephalus*.

The mandibular lateral line along the outer surface of the lower jaw is very clear in *Megalocephalus* material, but there is no sign of its continuation on the cheek region.

The fundamental structure of individual bones of the skull roof appears to be essentially similar in all loxommatids but a full description is possible only for this species.

Paired premaxillae meet antero-mesially in an interdigitating suture. Postero-laterally this relatively elongate bone forms the anterior border of the external naris and there is a pronounced flange forming a nasolabial groove from the naris to the jaw margin. Inside this groove a thin shelf of premaxilla extends backwards to suture with the anterior border of the septomaxilla, beneath which it has a short suture with the maxillary bone, which forms the lower border of the external naris. Post-mortem compression has often distorted the bones of this region, pushing the maxilla out laterally, but the arrangement of these elements is preserved in B.M.(N.H.) R585 and H.M. G15. 22.

The inner borders of the premaxillae suture with the internasal and nasal bones. Contact with the internasal is incomplete in some specimens, leaving small paired fenestrae through the dermal roof of the snout, presumably to accommodate elongated dentary tusks which must have projected onto the dorsal surface. This condition is paralleled in some modern species of *Crocodylus*, where the front pair of lower teeth are very long and perforate the tip of the snout, and in alligators where the fourth pair of dentary tusks may produce a similar perforation (Bellairs 1957). (See section on dentition below.)

These fenestrae are clearly apparent in the holotype (figure 6, plate 1) and in isolated premaxillae H.M. G15.34 and H.M. G15.35 and can also be seen from the ventral surface in

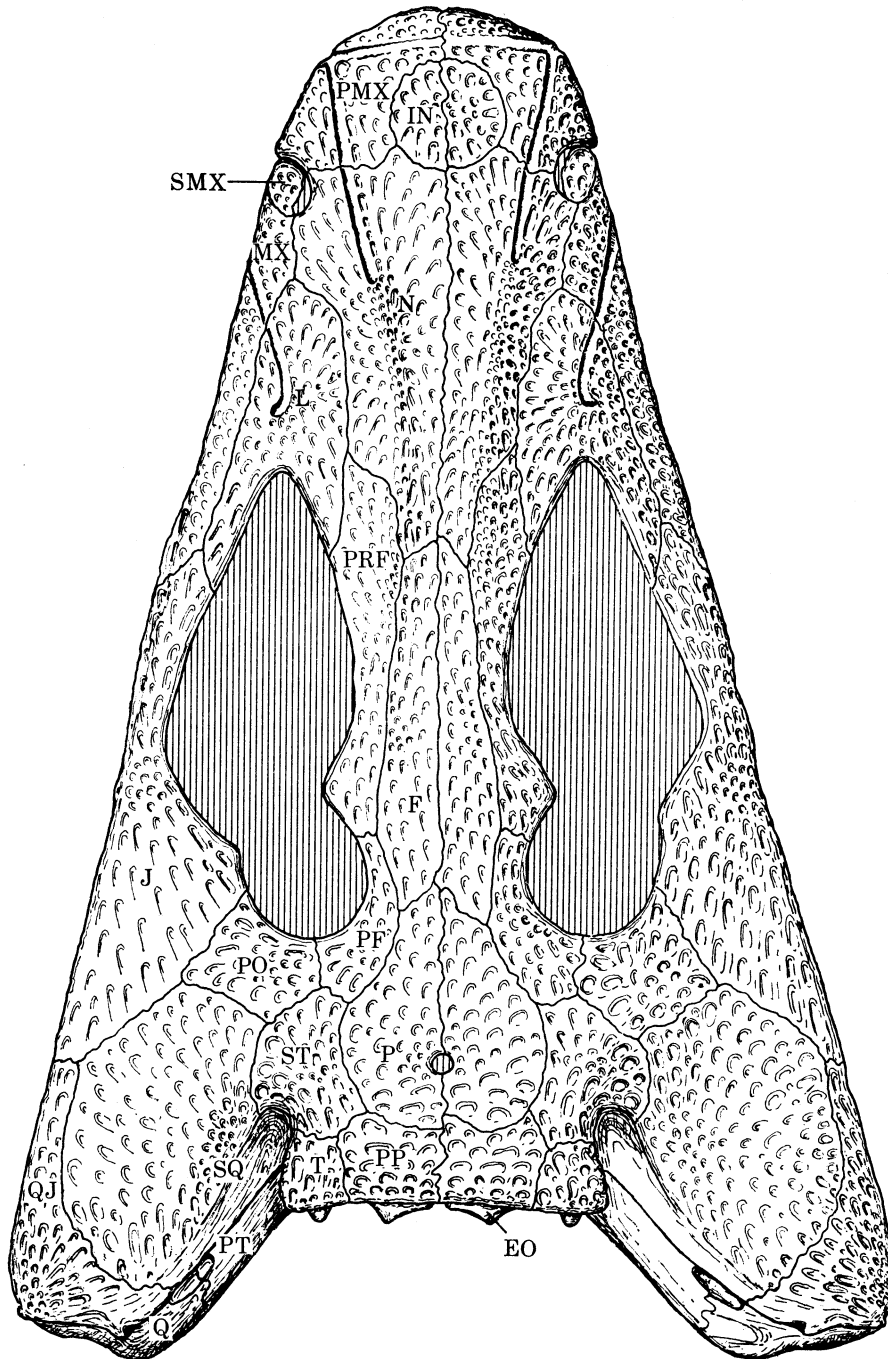


FIGURE 8. *Megalocephalus pachycephalus* (Barkas), composite restoration of the skull, dorsal view. Half natural size.

G.S. 28319. The only other specimens that show this region of the snout B.M.(N.H.) R585, H.M. G15.21 and H.M. G15.49, have no sign of fenestration.

The area between the postero-median borders of the premaxillae is occupied by either a single or paired median elements. In B.M.(N.H.) R585 there is a single internasal, while in H.M. G15.21, H.M. G15.22 and H.M. G15.49 there are paired internasal ossifications in this region. Such elements are possibly homologous with the rhipidistian postrostrals (Panchen 1970).

The nasal bones are extremely elongate in comparison with other loxommatid genera, the length of each being approximately four times the width. The frontals are also long and narrow and they suture posteriorly with the parietal bones, their orientation here being horizontal. Postero-laterally they suture with the postfrontal bones anterior to which they gradually assume a more vertical slope towards the snout.

The remaining midline bones, parietals and postparietals, together constitute the major portion of the skull table. The anterior part of the parietal lies in the interorbital region and is relatively narrow, suturing with frontal and prefrontal bones. The posterior half of the parietal broadens out to contact the supratemporal, the maximum breadth being about on a level with the pineal foramen.

The postparietals are relatively small compared with more primitive loxommatids. With a single exception the postparietal contacts the supratemporal antero-laterally and the tabular postero-laterally in a typical temnospondyl fashion. It is interesting to note that the condition is anomalous on the right side of the holotype where the anteromesial border of the tabular is somewhat extended and contacts the parietal, excluding the normal postparietal suture. There is no occipital flange on the postparietal as occurs in some temnospondyls, although ventrally there are thickened facets for the opisthotic.

The rest of the skull table is formed laterally by elements of the temporal series. In *Megalocephalus* there is no intertemporal bone, its position being occupied mainly by an anterior extension of the supratemporal, which also extends laterally to form the anterior border of the otic notch and sutures with the squamosal of the cheek region.

The small tabular occupies a postero-lateral position on the skull table. As in other loxommatids a small, rounded process, similar to that present in *Edops*, projects from the posterior margin and is probably the site of origin of part of the depressor mandibulae musculature. The amount of lateral extension of the tabular varies in individual specimens, being greatest in L1 of the Coope Collection.

The squamosal forms a major part of the cheek region. Its reflected mesial surface overlaps the quadrate ramus of the pterygoid, providing a smooth area for muscle attachment more than 1 cm deep. Anteriorly this area of unsculptured bone forms the side of the otic notch.

The quadratojugal occupies the postero-lateral corner of the skull. It has a short anterior suture with the jugal, but excludes this bone from the skull margin, as laterally it contacts the posterior border of the maxilla, as in *Loxomma*, but contrary to *Baphetes kirkbyi* Watson. The mesial and posterior borders of the quadratojugal are unsculptured and thicken to form a concave articular face which contacts a convex articulation on the quadrate. The unusual structure of these bones is shown in figure 11. Just anterior to its contact face with the quadrate, the mesial surface of the quadratojugal bears a deep notch, which when the two bones are correctly orientated forms a foramen, the palatoquadratum proprium (Bystrow 1939), between them. The foramen corresponds exactly to that in *Eryops* (Sawin 1941).

Anterior to the quadratojugal the lateral margin of the skull is formed by the elongate maxilla which attains its maximum depth (25 mm) behind the naris, before tapering to a short suture with the premaxilla inside the naso-labial groove.

The septomaxilla is a small ornamented bone, which in *Megalocephalus* is exposed superficially, so that it occludes most of the opening of the external naris. Laterally it sutures with the premaxilla and maxilla, which in effect partially closes the primitive laterally placed external nostril and restricts the narial opening to the dorsal surface of the skull. In *Edops* the

septomaxilla contacts the nasal postero-laterally, but this never occurs in *Megalocephalus*, nor, as far as is known, in any other loxommatid.

The tetrapod septomaxilla is believed to be the homologue of the processus dermintermedius of the rhipidistian lateral rostral bone (Jarvik 1942; Panchen 1967) and in *Ichthyostega* it carries the suborbital canal from the lachrymal onto the premaxilla. In *Megalocephalus*, however, the anterior part of this canal terminates on the maxilla lateral to its suture with the septomaxilla and is never found on that bone. The rhipidistian anterior tectal bone, prominent in the narial region of *Ichthyostega* (Jarvik 1952), is not present in the loxommatid skull, and has yet to be described for any temnospondyl.

The remaining bones of the dermal skull roof are those grouped as the circumorbital series, i.e. lachrymal, prefrontal, postfrontal, postorbital and jugal.

In *Megalocephalus*, as in many other long-snouted temnospondyls, the lachrymal does not reach the nostril. The bone is roughly triangular in shape, but its posterior border is indented by the front of the antorbital fenestra.

The prefrontal is a long, narrow bone which forms the mesial border of the antorbital fenestra. It expands laterally in its posterior quarter, indicating the front of the orbit proper. Behind this region it has a short suture with the postfrontal bone. Mesially it sutures with the frontal and posterior part of the nasal bone, and antero-laterally with the lachrymal. The condition differs from that of typical rhachitomes in that there is no contact with the jugal due to fenestration of the antorbital region.

Both the prefrontal and the small crescentic postfrontal, which forms the postero-mesial border of the orbit proper, can be seen in the lateral as well as the dorsal view of the skull, since they lie at a slight inclination to the midline bones.

The postorbital forms the postero-lateral border of the orbit. It is almost vertical, suturing with the jugal and squamosal of the cheek region and the supratemporal and postfrontal along its inner borders.

The anterior half of the elongate jugal forms much of the lateral wall of the antorbital fenestra. Posteriorly the element expands onto the cheek region to contact the quadratojugal, squamosal and postorbital. Laterally the jugal sutures with the maxilla, which excludes it from the skull margin.

The extremely compressed condition of most *Megalocephalus* specimens usually results in the palate being firmly attached to the ventral surface of the skull roof, so that the degree of sutural overlap between dermal bones cannot be determined for any one specimen, but where known, particularly in the cheek region, it appears to be quite considerable. In particular, the squamosal overlaps the supratemporal so that the latter does not extend around the otic notch on the ventral surface.

A single specimen B.M.(N.H.) R2364, shows an isolated skull table from the ventral surface. Facets for the braincase are essentially as described for *Loxomma*. The major difference is in the facet for the paroccipital process, which in this species extends onto the supratemporal instead of being restricted to the tabular.

A further feature which can be discerned from the ventral surface of the skull is the course of the naso-lachrymal duct. The lachrymal duct of labyrinthodonts is known in *Seymouria* (White 1939), where it is a closed tube running through the lachrymal bone on its way from orbit to naris, and also in *Eryops* (Sawin 1941) where it is believed to have occupied an open internal groove in both lachrymal and prefrontal.

The course of the duct in *Megalocephalus* is essentially similar to that of *Eryops* and is clearly apparent in H.M. G15.23, since in this skull the dermal bones between the orbital vacuities lift off and can be examined from below. The lateral projection of the prefrontal indicates the front of the orbit proper and presumably corresponded with the position of origin of eyelids and nictitating membrane, and consequently the lachrymal duct, as in crocodiles. The loxomatid duct begins in this region as a groove, which follows the mesial wall of the antorbital fenestra along the length of the prefrontal and on to the lachrymal bone. The bones have a lateral flange along the side of the vacuity and this curves over to form a tube-like structure, open only along its mesial side. An isolated palatine (H.M. G15.32) fits onto the right side of H.M. G15.23, completing the tip of the antorbital vacuity and also showing that the nasolachrymal duct ran into a posterior extension of the choana (probably the side wall the nasal capsule), on the palatine just mesial to the tip of the antorbital fenestration (figure 10*a*).

The dorsally situated paraquadrata foramen has already been described. It is presumed to be the site of entry of mandibular VII and associated blood vessels into the subtemporal fossa (Bystrow 1939). Ventrally (figure 11*b*) two foramina appear to correspond with the usual single accessory paraquadrata foramen (Bystrow 1939; Romer & Witter 1942). The nerve and blood vessels apparently passed into the thickened lateral margin of the quadratojugal, and reappeared 1–2 cm anteriorly. Their course continued forwards in a steep-sided groove from whence they presumably dipped ventrally towards the mandible.

Finally, the ventral surface of the jugal is interesting in that it forms an integral part of the antorbital vacuity. Along its ventro-lateral edge there is developed a relatively massive processus alaris (Bystrow & Efremov 1940). This structure is most clearly apparent in H.M. G15.23 (figure 10*a*), where it begins as a thin ridge alongside the posterior margin of the maxilla, gradually thickening to form a stout triangular buttress, which in life must have projected vertically for more than a centimetre below the general ventral surface of the jugal. The process is ovoid in a parasagittal plane over a distance of about 2 cm, anterior to which it continues forwards as a narrow ridge, lying approximately parallel with the maxilla, but with a valley for dentary teeth between the two. Thus the extended processus alaris is 8 cm long in H.M. G15.23 and nearer 10 in the large holotype skull (H.M. G15.22). In life this peculiarly long ventral process was in line and continuous with the solid lateral margin of the antorbital vacuity, also formed in part by a ventral extension of the jugal. Thus the side wall of the antorbital fenestra is continued back to the adductor fossa.

At the base of the processus alaris is a foramen, presumably for maxillary V (figure 10*a*). A further portion of this nerve can be traced in B.M.(N.H.) R2370. This skull is preserved in ironstone and canals are uncrushed and infilled with pyrites. Two tunnels, one presumably for the infra-orbital branch of V, run in the thickened mesial edge of the jugal, which forms the lateral margin of the skull. A small branch can be seen to leave the main tube in the region of the palatine tusk. The large tube then apparently runs forward between lachrymal and ectopterygoid and is again sectioned just mesial to the ectopterygoid tusk. Sections also indicate a tunnel running through the maxilla, presumably for maxillary and buccal rami of trigeminal V.

Palate and palatoquadrata

Three previous accounts exist of the palate of *Megalocephalus* (Hancock & Atthey 1875; Watson 1912; Watson 1926). All differ considerably as to the position of sutures, and even in the

number of bones involved in palatal structure. This is not surprising since reconstruction is based almost entirely upon the two most complete skulls from Newsham (H.M. G15.21, G15.22) and in both specimens a very thin, fine layer of cannel coal overlaid much of the bone surface and obscured detail. In addition, a black shellac-based glue had been used for

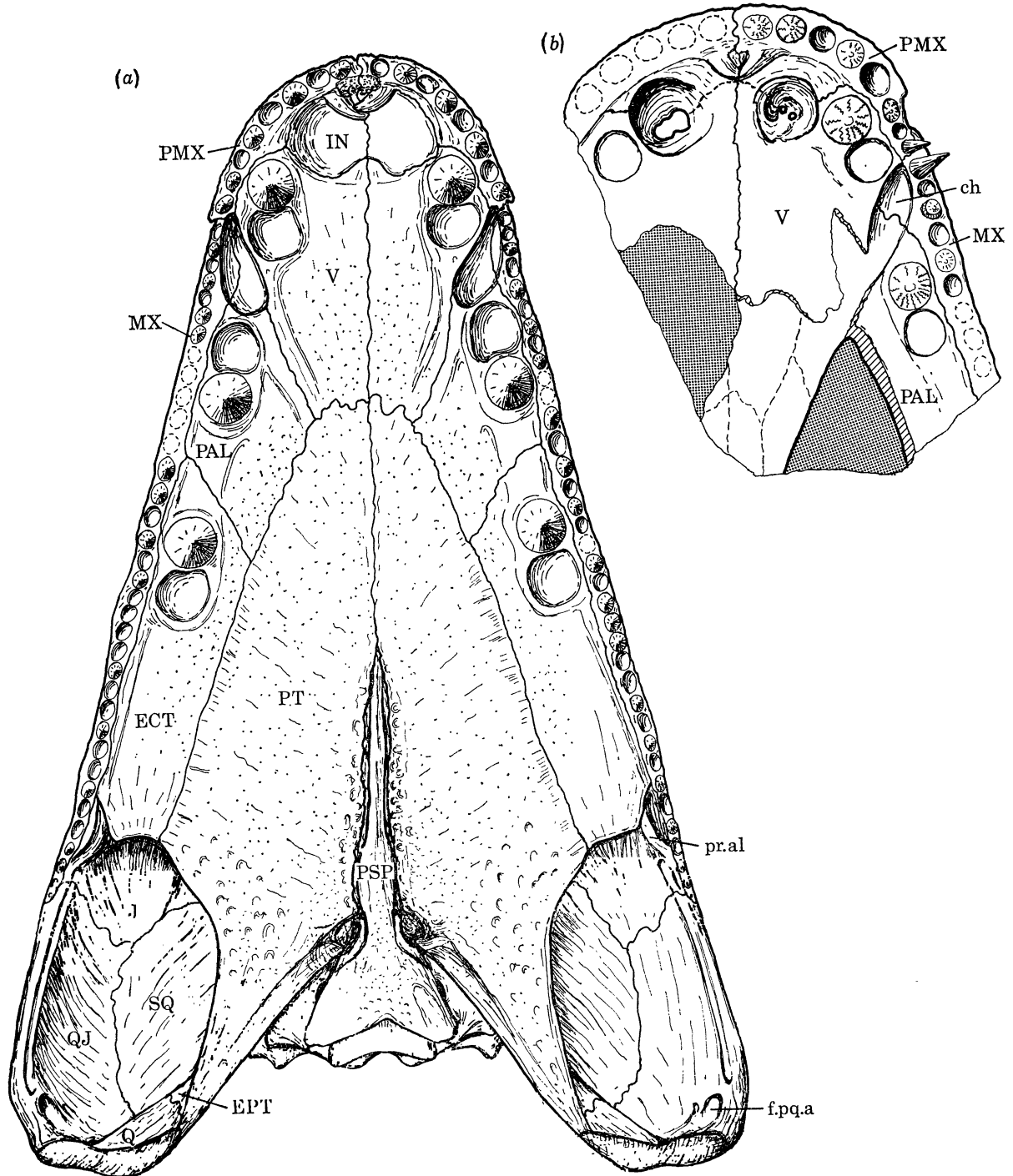


FIGURE 9. *Megalocephalus pachycephalus* (Barkas), palate, half natural size. (a) Composite restoration, (b) anterior region of G.S. 28319 in ventral view.

mending the specimens and to fill in areas where bone was missing. The solution had been varnished over large areas of both palates in order to prevent further damage to the bone surface, but this meant that subsequent preparation by normal mechanical means was impossible. The 'Airbrasive' machine has proved particularly useful in the cleaning of such delicate surfaces, and the palate of *Megalocephalus* can now be restored with reasonable certainty.

Palatal restoration (figure 9) is a composite of several specimens. As well as the two aforementioned skulls another specimen from Newsham H.M. G15. 23 (figure 10) has been cleared of matrix ventrally to show beautifully preserved posterior palatal elements. Other topotype material was prepared to confirm the position of sutures, and specimens from Derbyshire (Coope Collection L1, L3) were useful in this respect too. The anterior part of a skull from the Palace Craig Ironstone (figure 9*b*) also helps elucidate palatal structure and is interesting in that it differs in construction from Newsham specimens.

All specimens mentioned above have undergone dorso-ventral compression and only the horizontal palatal elements anterior to the basipterygoid process are retained more or less in their natural condition. Since the jaw rami are preserved in situ, the palate is obscured in the Coalbrookdale skull B.M.(N.H.) R585 but it is helpful in showing the vertical orientation of the quadrate ramus. *Megalocephalus* has a simple closed palate of primitive rhachitome pattern, as do other loxommatids. It is however more specialized than the other genera, since the anterior part of the palate is fenestrated for the reception of enlarged parasymphysial tusks of the dentary. Prior to this account, the anterior region of the palate was known only from Newsham material and all specimens from the Low Main Seam clearly possess a single, large, median fenestra. However, the Palace Craig skull, mentioned above, is peculiar in having double anterior palatal vacuities, each perforating the skull roof, the two circular apertures being separated ventrally by an anterior lappet of the vomers, which extend forwards to the premaxillae (figure 9*b*).

The choanae lie near the lateral margin of the skull behind the anterior fenestra(e), their axes being directed postero-medially. These vacuities are more elongate than in short-snouted loxommatids and reach a length of 45 mm in large skulls and maximum width of approximately 15 mm when the maxilla, which forms the lateral margin, is correctly orientated.

Since there is a primitive closed palate, the subtemporal fossae for the adductor musculature are the only other ventral openings. These are large, elongate vacuities. The ratio of length of subtemporal fossa to total skull length is known only for two individuals. In the large, type skull (H.M. G15. 22) it is approximately 1:3, whereas in the smaller Newsham specimen (H.M. G15. 21) it is nearer 1:2. The length of the fossa (posterior margin of ectopterygoid to posterior margin of quadrate) is known for a number of specimens and shows comparatively little variation, since increase in total skull length is due mainly to growth in the antorbital region.

Apart from the usual marginal dentition, tusk pairs are borne on the vomers, palatines and ectopterygoids and small denticles occur over much of the ventral surface of all palatal elements. An account of palatal and mandibular dentition is given separately below.

The premaxillae bear the anterior portions of the marginal tooth row. They have no palatal ramus and in *Megalocephalus* their stout rim forms the front of the palatal fenestra. On their ventral surface the postero-mesial border of each premaxilla is expanded to form a triangular buttress. These interlock with one another and in consequence each underlies the midline internasal suture in the roof of the fenestra. Reinforcement in this plane would appear to

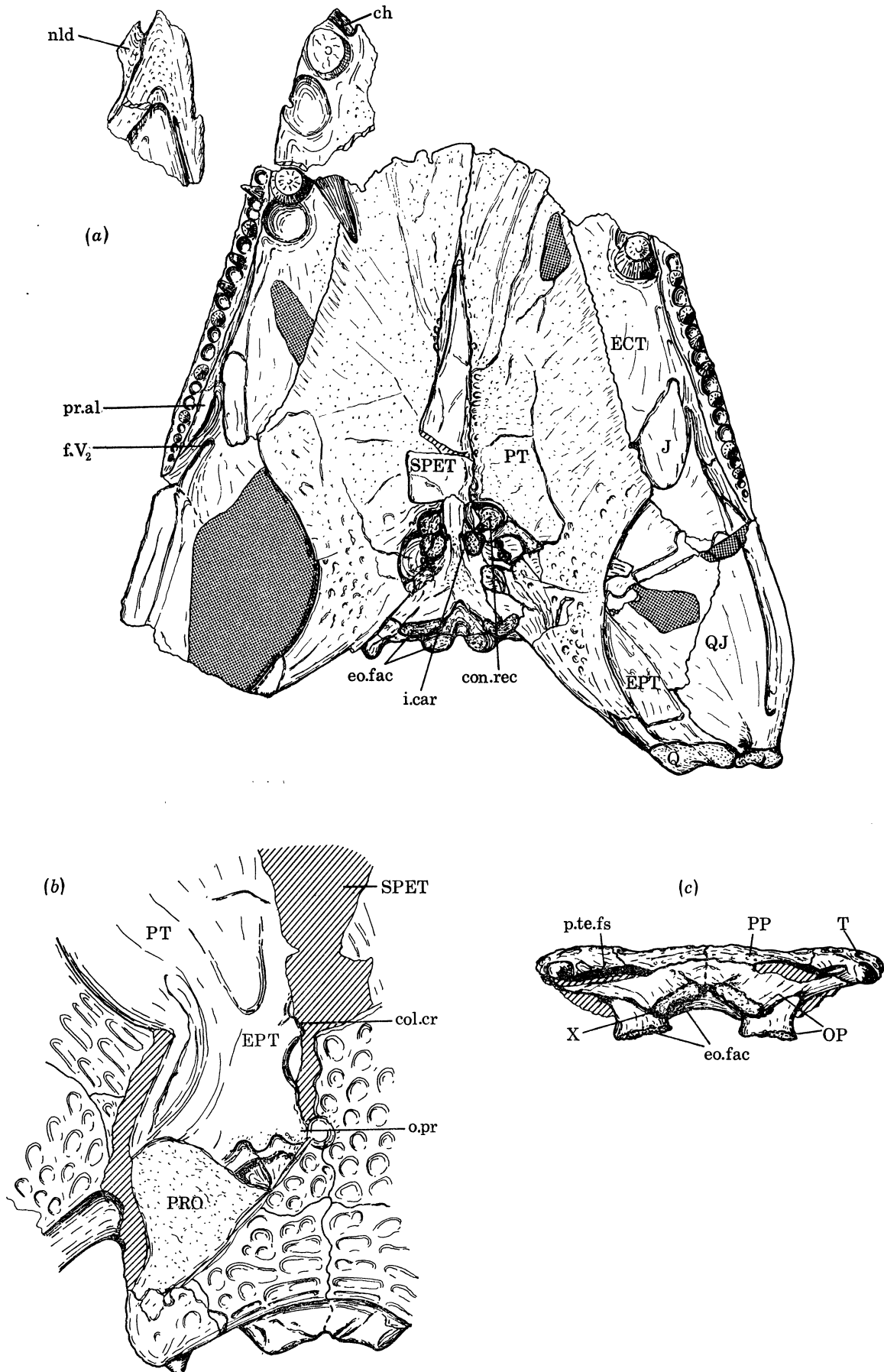


FIGURE 10. *Megalocephalus pachycephalus* (Barkas), H.M. G15. 23. (a) Palatal view with palatine G15.32 drawn in position and from its dorsal surface, half natural size. (b) Dorsal skull table with left supratemporal and parietal removed, (c) occipital view. Natural size.

be particularly important in genera where large premaxillary teeth are present. Often, one of the first premaxillary teeth is missing and the unequal pressure of the bite in such a situation would mean danger of sagittal shear were it not for the buttresses. In *Spathicephalus*, a related genus with a large number of small, even premaxillary teeth there is no such buttressing.

Just antero-ventral to the buttresses across the midline of the skull is a slightly inset rugose area which is subcircular in outline and approximately 1 cm in diameter. Sawin (1941) describes a similar structure in *Eryops*, whose function is unknown. Rugose pits also extend onto the buttresses, around the pedicel area of marginal and palatal teeth, along the mesial pterygoid border and the area around the subtemporal fossa. Such may represent thickened areas of attachment of the soft palate which must necessarily have been extremely thin over most of the palatal surface for the widely distributed palatal denticles to be functional. The postero-mesial margin of the premaxillary alveolar shelf sutures with the lateral margin of the vomer in the region of the first tusk. Posteriorly there is a short palatal suture between premaxilla and maxilla in the plane of the tooth row, causing a ventral separation of external naris and choana, as in *Ichthyostega*. The bones of this region are usually preserved apart due to lateral compression on the large vomerine tusks, which lie just inside the marginal tooth row. Contact between the various elements has, however, been retained in the holotype skull.

There is little exposure of the maxilla beyond the marginal tooth row. Behind the palatal suture with the premaxilla the bone gradually increases in depth to form much of the lateral wall of the choana and in this region there are two circular concavities, each about 5 mm in diameter, which receive the tips of a pair of enlarged dentary teeth. Posterior to the choana the maxilla sutures along its mesial edge with the palatine and ectopterygoid, contact with the posterior part of the latter bone being prevented by the processus alaris of the jugal. The tooth row in *Megalocephalus* extends back to the quadratojugal, which forms the lateral wall of the subtemporal fossa.

Passing to the palatal bones themselves, elongate vomers meet one another in a long midline suture. Antero-laterally each bone is much thickened to accommodate the roots of the large tusk pair and this stout, rounded rim of bone forms the posterior margin of the palatal fenestra. This sutures into the ventral surface of the dermal skull roof in the region of the internasal, nasal and premaxillary bones. Paired foramina occur in the lateral wall of the palatal fenestra between vomer and premaxilla, presumably allowing branches of nerve V to pass out of the bone to innervate the anterior palatal region.

The vomers normally extend forward slightly at their midline as a flattened lappet of bone, establishing firm contact with the ventral surface of the internasal ossicle(s). In the Palace Craig specimen (G.S. 28320) this vomerine lappet is enlarged and much thickened and runs forward to contact the buttressed region of the premaxillary bones producing a double palatal fenestra (figure 9b).

The thickened bone supporting the tusk pair continues backwards as a rounded buttress which forms the antero-mesial wall of the choana. The long lateral suture of the vomer with the palatine begins approximately two-thirds of the way down the length of the choana and posteriorly there is a firm, oblique interdigitated suture with the pterygoids.

There is little information on the structure of the dorsal vomerine surface. The isolated vomer H.M. G15. 33 shows a groove mesial to and running alongside the choana margin, which corresponds to the broken area 'pushed' in from the ventral surface in H.M. G15. 22. This is

a possible channel for the profundus branch of V, which is figured as occupying a similar position in *Benthosuchus* (Bystrów & Efremov 1940) and in *Megalocephalus* would appear to run out of one of the foramina near the base of the anterior vomerine tusk. All material has suffered compression and no impression of the cartilaginous nasal capsules has been traced with certainty on the vomers, but they must necessarily have been rather narrow anteriorly, since in the middle region of the skull the vomers suture with the dermal skull roof.

The palatine also possesses a single tusk pair on a thickened area of bone, which extends forwards forming the posterior wall of the choana. Part of an isolated right palatine from Newsham (H.M. G15.32—now associated with skull H.M. G15.23) shows some curious features of the dorsal surface of this element. Much of this surface is roughened and presumably in life would be intimately associated with the dermal roofing bones—lachrymal and maxilla. A sunken, smooth triangular area indicates the anterior limit of the antorbital fenestra. The anterior and lateral walls of the area slope up as a dorsal flange that in life sutured with the lachrymal, forming the solid antero-lateral wall of the fenestra. Alongside this structure runs a groove which was roofed by the lachrymal and formed a tube presumably for the infra-orbital branch of nerve V. The nerve apparently ran forward lateral to the choana between the palatine and maxillary bones. Another feature of this palatine specimen is that the posterior wall of the choana extends backwards as a rounded smooth-sided channel for a distance of about 2 cm, the cavity so formed running mesial to the antorbital fenestra, and connecting with the nasolachrymal duct. The channel, which is about a centimetre deep, would seem to represent the lateral edge of the nasal capsule, which must necessarily have been a comparatively large structure abutting against the sphenethmoid mesially, as in modern Amphibia. (See discussion of braincase.)

The third pair of tusk-bearing lateral palatal bones are the ectopterygoids. Watson (1926) suggested that these elongate elements might actually consist of two separate ossifications, an anterior ectopterygoid bearing the tusk pair and a small posterior toothless element, corresponding to the transverse of his 1912 description. However, since there is no homologue of the latter bone in the crossopterygian skull, doubt is cast on this hypothesis. It is true that the posterior third of the ectopterygoid is often sheared off, but the explanation would seem to lie in the relationship of this bone to the surrounding elements. The anterior part of the ectopterygoid is firmly held by its suture with the palatine and also by a stout dorsal connection with the skull roof. A dorsal median ridge of the ectopterygoid unites with part of the ventral jugal flange to continue the solid lateral wall of the antorbital fenestra. Mesially the ectopterygoid is underlain by the pterygoid. Laterally it contacts the maxilla along most of its length, but since there is a steep-sided groove for the reception of the dentary tooth row between these two bones they are not firmly sutured. The posterior part of the bone is separated from the maxilla laterally by the processus alaris of the jugal and during post-mortem compression is pushed against this vertical buttress and sheared away. Since the pterygoid suture is overlapping and relatively weak this bone often remains undamaged, the ectopterygoid section sliding dorsal to it, which helps give the impression that it is a separate element.

The large pterygoids form a major area of the palate, their horizontal palatal rami meeting anteriorly in a midline suture. Dorso-ventral compression has pushed the sphenethmoid between the palatal elements, but it would appear that for the posterior two-thirds of its length the palatal ramus of the pterygoid was separated from its fellow by the braincase and parasphenoid. The bone is thickened and considerably pitted along its mesial edge, but away from the midline

bears a shagreen of fine denticles. Anteriorly the pterygoids are firmly fixed by a strongly interdigitating suture with the vomers and anterior palatines while laterally there is an overlapping suture with the ectopterygoid.

The palatal ramus of the pterygoid is best preserved in G15.23 (figure 10). It is somewhat thickened in its central region where it becomes intimately associated with the epipterygoid to form the conical recess of the basal articulation. The rim of the conical recess as viewed from the palatal surface is apparently the thickened mesial edge of the pterygoid ossification. The cavity of the recess, assumed to be epipterygoid in origin, has a concave roughened surface. The anterior rim overlapped and articulated with the ventral surface of the basiptyergoid process. The pterygoid slopes vertically to form the lateral wall of the recess which contacted a second, more lateral articular face of the basal process. (See braincase description.)

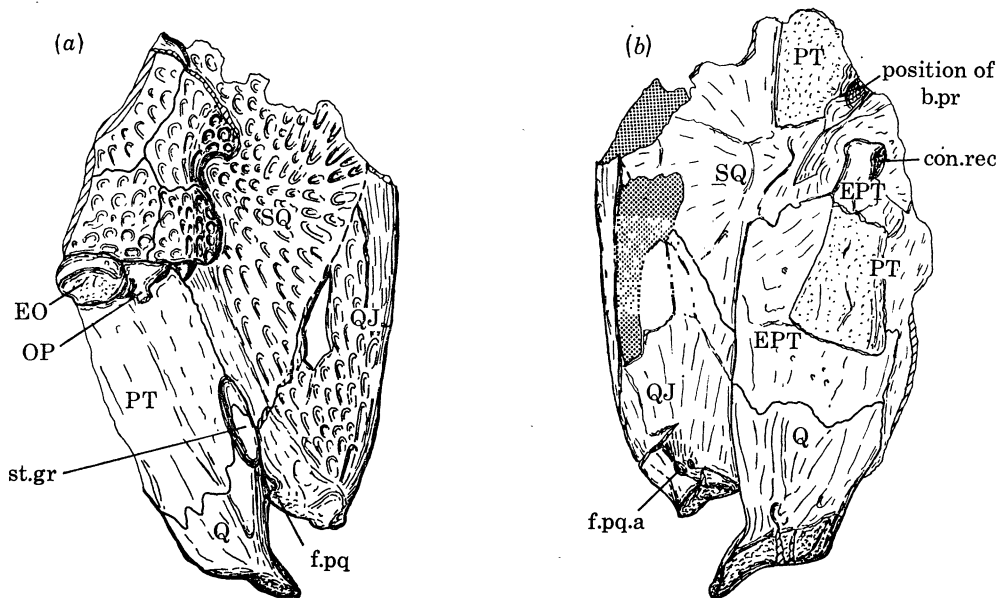


FIGURE 11. *Megaloccephalus pachycephalus* (Barkas), H.M. G15.27. Half natural size: (a) dorsal view, (b) ventral surface. The palatoquadrate has moved posteriorly to expose articular surfaces between the quadrate and quadratojugal.

In the undistorted skull the pterygoid rotates through its length so that its quadrate ramus, which forms the mesial border of the subtemporal fossa, is a vertical sheet of bone. The deep quadrate ramus, preserved undistorted only in B.M.(N.H.) R585, projects below the dermal cheek region in lateral aspect, as restored in *L. acutirhinus* (figure 3b).

In the mesial cheek region the quadrate ramus of the pterygoid is overlapped by the border of the unornamented descending process of the squamosal and along its posterior border it firmly sutures with the antero-mesial extension of the quadrate. The relationship between these elements is best seen in H.M. G15.27 (figure 11), in which the quadrate and pterygoid ramus have been pulled back, the latter having slid along its squamosal contact. This specimen shows a well-defined pit, almost 2 cm in length, between the pterygoid and the quadrate, which Watson (1926) noted must have faced towards the otic region in the uncrushed skull. It is possible that this depression housed the distal end of a long cartilaginous quadrate process of the stapes (White 1939; Parrington 1948).

Elements of the primary palatoquadrate arch, i.e. epipterygoid and quadrate ossifications enter into a complex association with the pterygoid, the three bones apparently functioning as a unit, allowing slight mobility of the palate on the basipterygoid process. (See section on functional morphology.)

The structure of the epipterygoid is not well known, since it is generally compressed between the skull roof and the pterygoid, but two specimens, H.M. G15.23 and H.M. G15.27, give some indication of its general form. In the skull H.M. G15.23 the dermal bones of the inter-orbital region and a section of the left half of the skull table lift off to expose the dorsal surface of the epipterygoid from the region of the conical recess forwards (figure 10*b*). The relatively horizontal anterior sheet of the epipterygoid apparently co-ossifies with the dorsal surface of the palatal ramus of the pterygoid and there is no clear line of suture between the two. It is probable, however, that the epipterygoid ossification corresponds with the thickened area of bone which extends rather irregularly for a distance of between 1 and 2 cm in front of the level of the anterior margin of the conical recess. This would correspond to the known limit of this ossification for *Loxomma*.

The central region of the epipterygoid is considerably thickened and ventrally forms the wall of the conical recess. In G15.23 the palatoquadrate has been pushed forwards away from the basipterygoid, and the hemispherical cartilage-finished surface of the epipterygoid is clearly apparent. Just anterior to the conical recess, on the dorsal surface, is a slight projection which may represent the base of the columella cranii (ascending process). The latter is presumed to have continued in cartilage as a slender rod contacting the skull roof in the region of the parietal bone.

Posterior to the columella cranii and somewhat dorsal to the conical recess, the epipterygoid bears a number of articular facets, which are difficult to interpret since they have been compressed into a single plane, whereas their natural relationships were probably somewhat different. The innermost facet, which in life would lie dorsal to the others, is thought to be the otic process. The other, rather more ventral facets would contact small articular surfaces of the braincase, dorso-lateral to the basipterygoid process. Similar facets are described for *Edops* (Romer & Witter 1942).

The epipterygoid also has an extensive quadrate ramus, lying morphologically dorso-lateral and thus internal to the pterygoid and closely following the contour of the vertical pterygoid ramus. It can best be seen from H.M. G15.27 where the mesial wall of the subtemporal fossa has been folded out, to show particularly well the long interdigitating suture between quadrate and epipterygoid (erroneously figured by Watson 1912 as squamosal). The palatoquadrate has been pulled back and has come to lie across the squamosal, with which it did not apparently suture. It seems probable that slight movement could have occurred between the mesial border of the palatoquadrate and the descending flange of the squamosal if the former structure were slightly mobile on the basipterygoid process.

The extent of the quadrate ramus of the epipterygoid may almost certainly be interpreted as a primitive condition. It is comparable with that described by Panchen (1964) for the contemporary anthracosaur *Palaeoherpeton* ('*Palaeogyrinus*') and is comparatively greater than that described for *Edops* (Romer & Witter 1942) where the quadrate ossification is more extensive. Later labyrinthodonts are characterized by progressive reduction of the epipterygoid.

From H.M. G15.27 it is apparent that the quadrate ossification was not firmly sutured into the dermal skull roof, as in later labyrinthodonts. Mesially the quadrate meets the pterygoid

in a strongly interdigitated suture, with the pit supposedly for the stapedal process lying between the two bones. Laterally the quadratojugal overlaps the quadrate, the paraquadrate foramen being formed by notching of the former bone. The quadrate bears an articular surface which faces antero-laterally and is cupped by a corresponding surface formed by the thickened posterior rim of the quadratojugal.

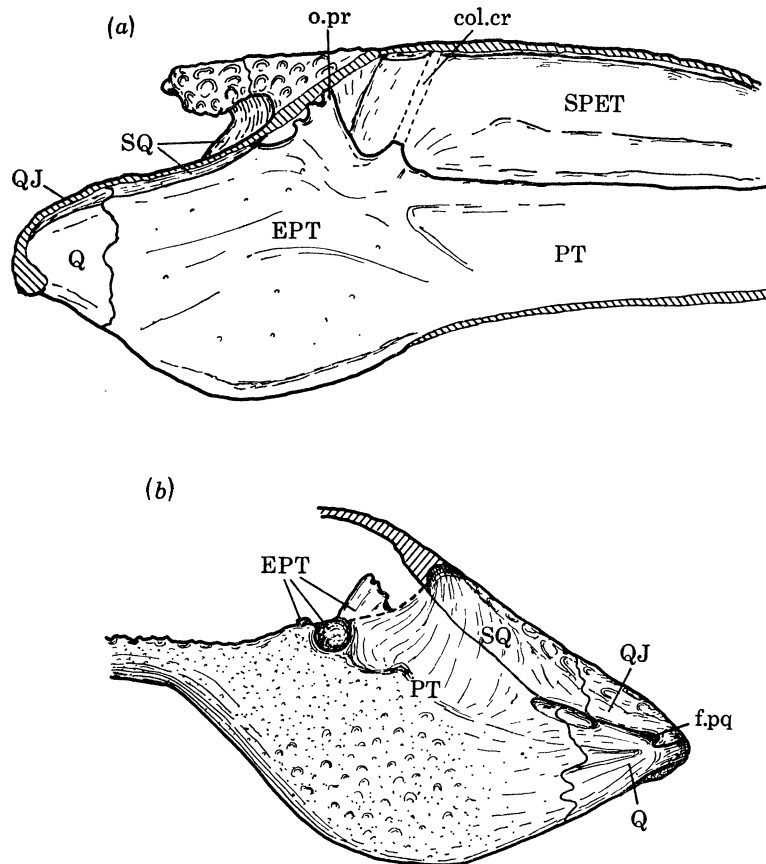


FIGURE 12. *Megalocephalus pachycephalus* (Barkas), composite reconstruction of the palatoquadrate: (a) lateral, (b) mesial view. Half natural size.

The second articular face on the quadrate is the cylindrical surface for the concave lower jaw articulation. Its position in occipital aspect can be determined from B.M.(N.H.) R585. The bearing surface begins near the lower margin of the bone, being obliquely orientated at first, but gradually attaining a horizontal position along the second half of its length (figure 13 a).

Braincase and parasphenoid

The neurocranium of *Megalocephalus* is not well preserved in any single specimen. The ventral surface of the braincase responded well to cleaning in a number of Newsham skulls, but although individual bones were in an excellent state of preservation all had been subject to dorso-ventral flattening and yielded comparatively little information on gross morphology. The Coalbrookdale skull B.M.(N.H.) R585 yielded no evidence beyond broken bones around the back of the posttemporal fossae, the neurocranium apparently having been lost soon after the death of the animal.

Because of the paucity of material Watson (1926) attempted no restoration of the braincase of *Megalocephalus*, apart from the occiput. The present reconstruction (figure 13) is a composite of information from many specimens, but is based in outline upon the braincase impression on the ventral surface of B.M.(N.H.) R2364. The outline was confirmed by X-ray photographs of H.M. G15.21, since this relatively dense area showed up quite clearly. The neurocranium of *Loxomma* proved useful for confirmation of doubtful features in the present genus and those not apparent from any specimen of *Megalocephalus* have necessarily been restored from the former. The two are essentially similar in general form and thus description in this genus will concentrate upon those features which add to the overall knowledge of a loxommatid braincase. In particular the parasphenoid, basiptyergoid process and occipital region warrant a complete description since this was not possible for *Loxomma*.

As in *Loxomma* there is little expansion of the cultriform process of the parasphenoid, which extends forward beneath the narrow sphenethmoid region. It is triangular in section and is somewhat less than three-quarters of a centimetre maximum width in the large holotype skull where it has been preserved pushed over to one side and is partly overlapped by the sphenethmoid. In H.M. G15.23 (figure 10) the anterior extension of the parasphenoid has apparently sheared off the sphenethmoid, part of which has been pushed through onto the ventral surface. When present however the parasphenoid would only be exposed on the palatal surface up to the level of the ectopterygoid tusks, since the pterygoids meet in midline suture further anteriorly. The extent of the parasphenoid anterior to this point is not known for any specimen of *Megalocephalus* and although it is known for *Loxomma acutirhinus*, in this species the anterior parts of the pterygoids are missing. However, evidence from other labyrinthodonts indicates that 'the anterior end of the process primitively extended forward dorsal to the anterior ends of the conjoined pterygoids and vomers' (Romer 1947). Such is likely to be the case for loxommatids since the parasphenoid is structurally primitive in other features. In advanced labyrinthodonts the cultriform process is considerably broader and flatter and with expansion of the interpterygoid vacuities becomes exposed along the whole of its length.

Large well-defined foramina associated with the internal carotid arteries pierce the parasphenoid near the base of the cultriform process, which is comparatively slender in this region and bears a shagreen of denticles. Posterolaterally the parasphenoid expands to ensheath the basisphenoid core which is exposed here only as the complex articular bearing-surface of the basiptyergoid process. Thus the basic construction of the basiptyergoid process is virtually the same as that of *Edops* (Romer & Witter 1942) and could represent the primitive temnospondyl condition. In more advanced temnospondyls such as *Eryops*, the parasphenoid sheath sutures with the pterygoid thus immobilizing the articular region and the extent of this contact increases throughout temnospondyl evolution. In anthracosaurs, however, it is likely that the parasphenoid never enters into the construction of the basiptyergoid process (Shiskin 1968; Panchen 1970) and this may be one of the fundamental differences between primitive members of the two labyrinthodont stocks.

Posterior to the basiptyergoid processes the parasphenoid continues to expand laterally and curve sharply upwards along its margins, presumably fusing into the side walls of the otic capsules, which it floors ventrally. The flattened state of all specimens means that the exact structure of this region is not known. Posteriorly the parasphenoid ensheaths the anterior region of the basioccipital, but from its broadly expanded shape it seems likely that the lateral edges end in a broad free rim, as is described by Romer & Witter (1942) for *Edops*. Watson (1926)

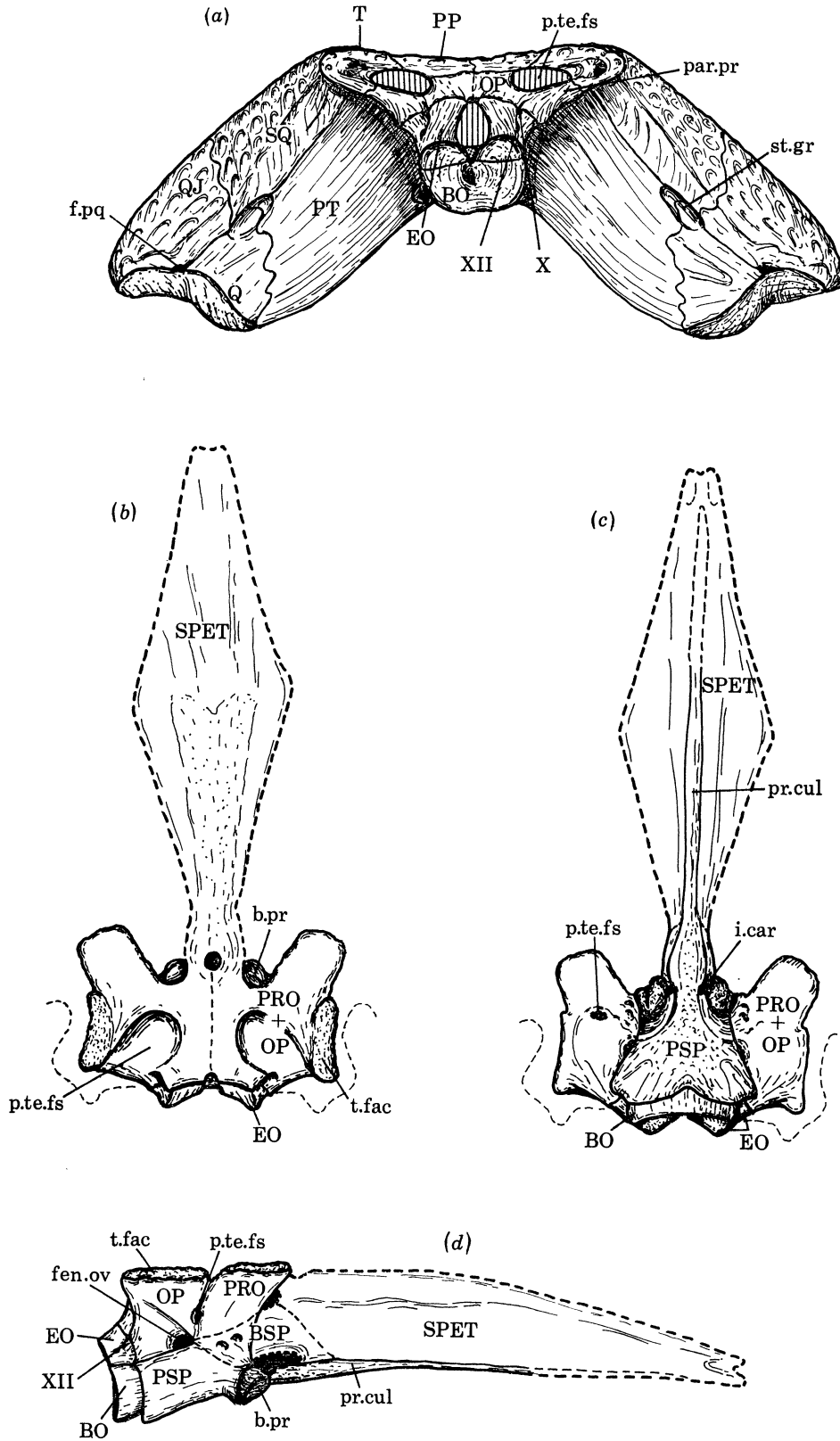


FIGURE 13. *Megalocephalus pachycephalus* (Barkas), composite reconstruction of braincase: (a) occipital, (b) dorsal, (c) ventral, (d) lateral view. Half natural size.

commented on rounded eminences in the lateral region between the parasphenoid and basioccipital, which he cites as the first trace of the tubera basisphenoidales for the recticapitis muscles. The smooth triangular depression extending from the postero-lateral corner of each side of the parasphenoid probably also indicates an area of muscle insertion, and it seems likely that the neck musculature was inserted around this general area. Denticles occur over much of the midregion of the otic expansion of the parasphenoid.

The occiput has suffered considerable compression in all material of *Megalocephalus* in which it is preserved, but can be reconstructed with reasonable certainty when information is compiled from a number of specimens (figure 13a).

The occipital region is formed partly from structures of the posterior walls of the otic region, against which abuts the occipital arch proper, the whole forming a surface which is roughly triangular in shape. Noticeable features of the occiput are the large post-temporal fossae which characterize the temnospondyl stock, but are absent in most anthracosaurs. Also there is a large foramen magnum bounded ventrally by a massive rounded concave occipital condyle, of primitive tripartite construction, as is characteristic of other primitive temnospondyls (e.g. *Edops*, *Dendrerpeton*), anthracosaurs and seymouriamorphs.

In common with other primitive labyrinthodonts, but in contrast to the advanced temnospondyl condition, the loxommatid basioccipital forms the major part of the articular surface of the condyle. In the large holotype skull the width of the bone is approximately 3.5 cm and the height about 1.5 cm. Dorsally there are contact surfaces for the paired exoccipitals, the posterior faces of which form the upper limits of the condyle. An isolated basioccipital (H.M. G15.29) reaches a depth of 2 cm. The ventral surface is deeply striated and in life would have contacted the dorsal surface of the parasphenoid. Laterally rounded articular areas for the exoccipitals are apparent.

The exoccipital, best preserved on the left side of the holotype, is a complex element with a number of surfaces. Posteriorly there is a wedge-shaped articular face, forming the top part of the condyle. Ventrally the bone sutures with the basioccipital. From the condylar area, the exoccipital extends anteriorly at an angle of about 45° as a massive column which bifurcates into two columns lying in different planes. The more anterolateral has a cartilage-finished surface which contacts the paroccipital process of the opisthotic. The more postero-mesial is slightly concave and forms the smooth side wall of the foramen magnum. The foramen for nerve XII lies between the two main struts, its presence in this element being a primitive (crossopterygian) character lost in most later labyrinthodonts.

In loxommatids the opisthotics play an important part in occipital construction. Their structure in this respect can be seen most clearly in H.M. G15.23 (figure 10), in which the exoccipitals and basioccipital have been squeezed out and lost, presumably as the parasphenoid was pushed in by compression. Compression has also closed up the post-temporal fossae and pushed the opisthotics slightly forward, but otherwise the region is relatively undistorted, and together with the occipital arch from the holotype forms an excellent basis for occipital reconstruction.

In the anthracosaur skull the area above the foramen magnum is occupied by a median supraoccipital bone, separating the opisthotic ossifications. Watson (1926) believed that this was a primitive feature for all labyrinthodonts and featured a similar ossification in his occipital reconstruction of *Megalocephalus* ('*Orthosaurus*'), the evidence cited being H.M. G15.23. The area is obviously completely ossified in this form, but no sutures are apparent. In embryonic

structure the region in question is occupied by the synotic tectum. In non-loxommatid temnospondyls the area is variably covered by descending flanges of the postparietals, or by exoccipital extension. In many cases the central part is unossified, presumably filled by cartilage in life. The cartilage area is usually tentatively labelled supraoccipital since the structure was believed to be a feature of primitive temnospondyls, namely loxommatids.

It seems unlikely however that there was a discrete element in the region of the synotic tectum in the loxommatid skull. This conclusion is based not on *Megalocephalus* material but on specimens of the related loxommatid genus *Baphetes*, in which a clear midline suture can be seen between paired opisthotic bones (see description of *B. kirkbyi*). Thus it seems probable, as Romer suggested in 1947, that the supraoccipital bone is an anthracosaurian and reptilian feature that possibly never appeared in the temnospondyl stock.

In occipital aspect the opisthotic can be seen as an extensive area of bone, extending as the paraoccipital process from the ventro-lateral margin of the tabular, flooring the post-temporal fossa and dividing into two short, stout postero-ventrally directed columns, each bearing a cartilage-finished attachment area for similar surfaces on the exoccipital.

The outline of the post-temporal fossae and the grooves and roughened attachment areas for the dorsal surface of the braincase indicate that the otic region is essentially of similar construction to that already described for *Loxomma*. Material of *Megalocephalus* adds no further important information about this region although further details on the precise construction of the otic capsule are apparent from a specimen of *Baphetes kirkbyi* (see below).

The basisphenoid is well known in ventral aspect as far as structure of the basiptyergoid process is concerned, but because of dorso-ventral flattening of the braincase material, it is not known to what extent the basisphenoid entered into formation of the lateral wall of the basiptyergoid process.

The basiptyergoid process is well preserved in most specimens, but has suffered least distortion in H.M. G15. 23, where it is clearly visible since the pterygoids have been pushed well forwards, whereas in most other specimens they still partly envelop the articular region. The process is bounded mesially and posteriorly by the ensheathing parasphenoid, but the basisphenoid core forms the complex anteriorly facing articular surfaces for the palatal structures. The main articular surface lies along the longitudinal axis of the process at an angle of approximately 45° to the vertical and would articulate with the thickened antero-ventral rim of the conical recess. The surface is in the region of 5 mm wide and 10 mm long. The lateral side of this articular face rises sharply in the vertical plane and then levels out to form a second articular surface of similar proportions to the first, the two being united at their posterior border. This second articular surface slopes at about 20° to the vertical and faces rather more laterally than the first. It accommodates the postero-lateral rim of the conical recess. The palatal structure would have slid along the ridge formed by the two basisphenoid surfaces, but could not have rotated round the process.

In the braincase of *Loxomma* it would appear that the basisphenoid is extensively ossified anterior to the basal process in the laterosphenoid region of the braincase, in primitive temnospondyl fashion, and limited evidence suggests that this is also true of *Megalocephalus*. In H.M. G15. 23 the line of suture between parasphenoid and basisphenoid appears to follow the mesial wall of the basal articulation which also forms the lateral side of the groove presumed to be for the palatal artery. The line between the two bones can be traced for about a centimetre but no further, due to breaks and distortion in the specimen. Thus the element extended

forward dorso-lateral to the cultriform process of the parasphenoid for at least a short distance. Unfortunately, due to compression of all specimens, none of the foramina that one would expect to be present can be traced in this region.

It seems probable that the basisphenoid also had an extension dorso-lateral to the basal process and continuous with the otic region of the braincase. This area is visible in H.M. G15. 23, on the right side in palatal view, and is remarkable in that it bears a pair of small articular facets, which were presumably cupped by the epipterygoid processes which lay dorsal to the region of the conical recess.

Knowledge of the sphenethmoid region of the braincase is limited. As in *Loxomma* this cartilage bone is ossified to a level slightly beyond the tip of the antorbital vacuity. Much of the ossification forms an interorbital septum, which can be observed from the palatal surface of H.M. G15. 23 since it has been pushed between the pterygoids. This sheet of bone, which is narrowly V-shaped in section, apparently reaches a depth of 3–4 cm in the interorbital region of the above specimen, but this has decreased to approximately 1 cm when seen in section in the incomplete skull B.M.(N.H.) R2370 near to the front of the antorbital vacuity, in which region it is more broadly V-shaped. The septum expands dorsally, presumably to accommodate the olfactory tracts, and becomes closely applied to the underside of the skull roof. The area of attachment runs as a band of about 1 cm width anterior to the pineal foramen along the mid-region of the frontal bones, near the level of the border of the orbits proper, where it extends laterally. This lateral wing probably represents the area of maximum width of the sphenethmoid, which apparently tapers anteriorly.

Nasal capsules are not ossified in any known labyrinthodont, but in *Megalocephalus* there is evidence at least of the proportions of these structures. From the dorsal palatal structure already described they appear to be surprisingly long, but relatively narrow, extending mesially and posteriorly from the choanae. Their posterior margin lay mesial to the front of the antorbital vacuity and thus they would abut against the sphenethmoid, which was ossified to this level. Therefore it would seem that in *Megalocephalus* the nasal capsules were comparatively larger than in *Eryops* where a possible outline is apparent (Sawin 1942). However, on the ventral surface of the type skull roof of the primitive anthracosaur *Palaeoherpeton*, along the anterior edge of the orbit are well defined rims which flare out and thicken to enclose a rounded groove in their antero-mesial surfaces (Panchen 1964). The groove is approximately continuous with the front of the sphenethmoid and as such could well indicate the rounded posterior margin of the nasal capsule, a structure of similar proportion and extent to that of the loxommatid here described.

Lower jaw

The general structure of the lower jaw is essentially as figured by Watson (1926). Each ramus is relatively deep throughout its length, tapering slightly towards the symphysis in lateral view, but not to the same extent as the deeper, more massive jaw of contemporary anthracosaurs.

There is no retro-articular process and thus the glenoid fossa of the articular is more or less terminal. This articulation is well above the level of the general surface of the dentary tooth row, since the quadrate condyle of the skull is relatively high.

The well defined mandibular lateral line canal follows the rounded postero-ventral edge of the jaw ramus, passing forward to meet its fellow in the symphyseal region.

A major feature seen in mesial and dorsal aspect (figures 14*b* and 15) is the adductor fossa,

a steep-sided cavity into and around which the adductor mandibuli muscle mass inserted. The fossa is walled laterally by the surangular, which slopes down from the articular region. There is no development of a high convex surangular crest, a prominent feature of the lower jaw both of anthracosaurs and of many temnospondyls. Anteriorly the fossa tapers and is bounded by the posterior margin of the posterior coronoid, at the level of the back of the tooth row. The

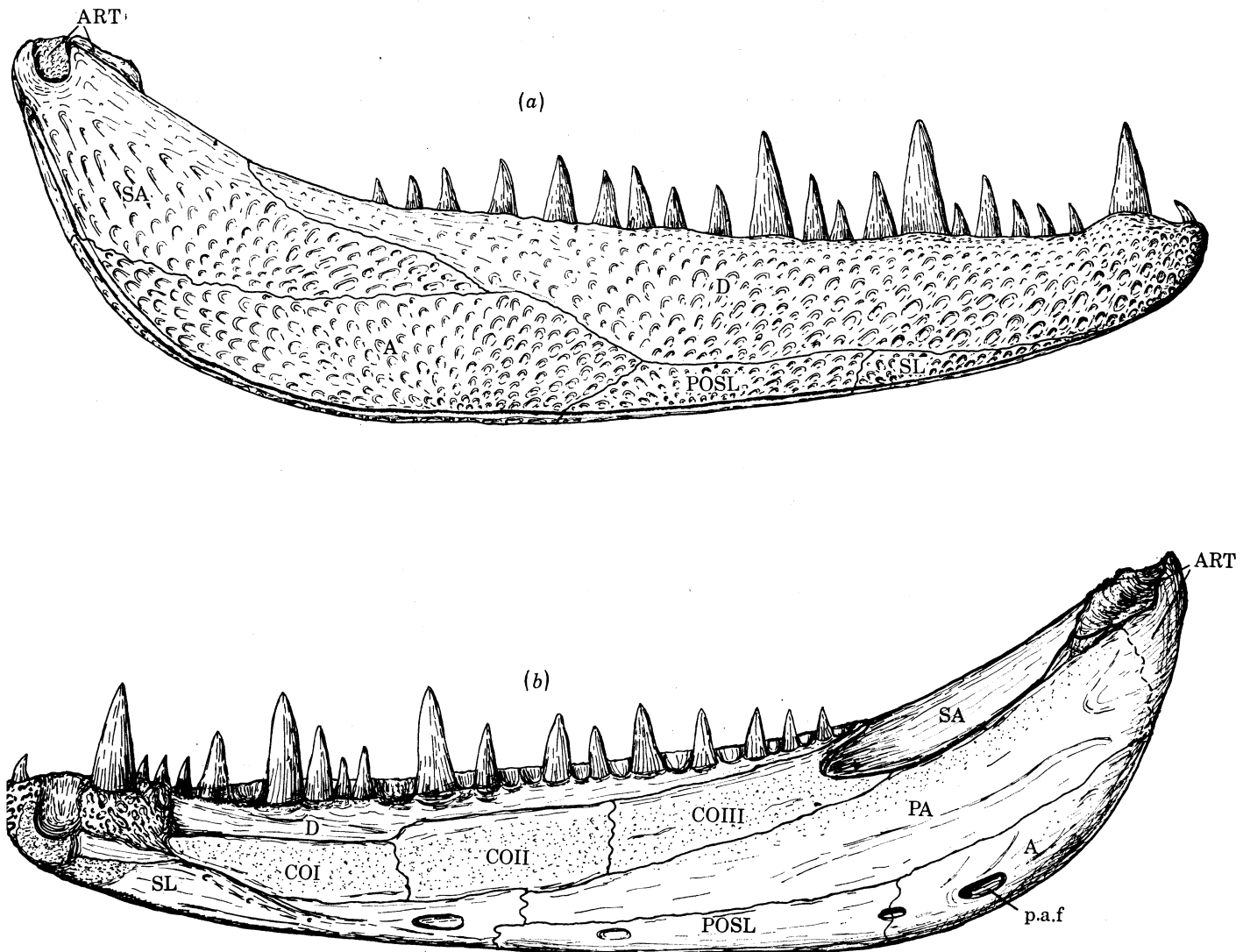


FIGURE 14. *Megalocephalus pachycephalus* (Barkas), composite reconstruction of right jaw ramus. (a) Lateral, (b) mesial view. Half natural size.

cavity, however, extended forwards in the tunnel formed between the inner and outer walls of the ramus as the Meckelian space (seen ventrally in B.M.(N.H.) R585), which may have been partially occupied by Meckel's cartilage (Nilsson 1944).

In the anthracosaur jaw the two enormous Meckelian fenestrae are characteristic features of the mesial aspect (Watson 1926), and a single large fenestra has similarly developed in a number of temnospondyl groups (Romer 1947). In loxommatids, however, there is no real fenestration, each ramus being pierced ventro-mesially by a number of relatively small foramina. The position and relative size of these varied in the specimens examined, but in all cases there seemed

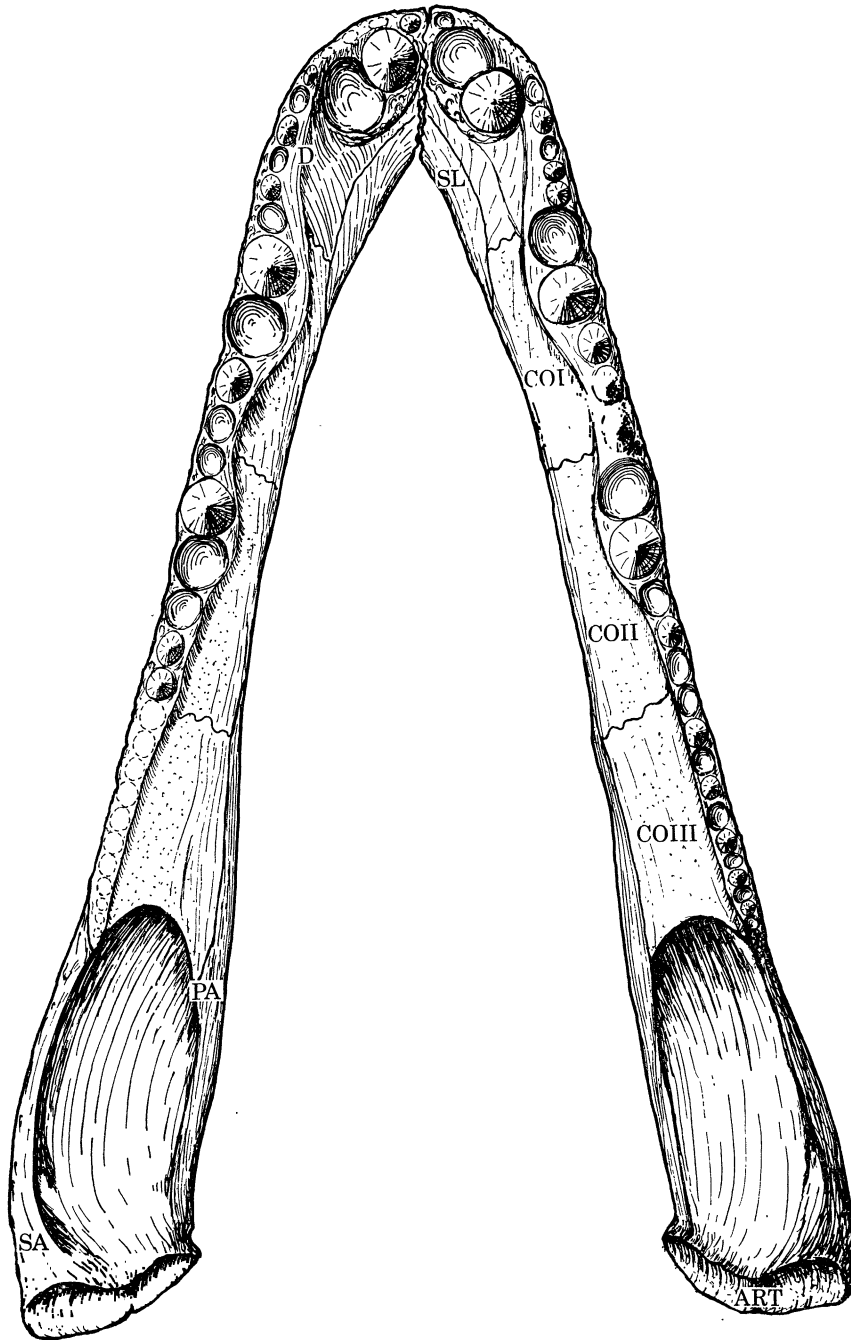


FIGURE 15. *Megalocephalus pachycephalus* (Barkas), composite restoration of lower jaws in articulation in dorsal view. Half natural size.

to be four main foramina, with variable small perforations, presumably for nutrient vessels. Nilsson (1944) equated the anterior two, perforating the splenial and postsplenial, with the anterior Meckelian foramen of other labyrinthodonts. The next, between postsplenial and angular he believed to be the posterior Meckelian foramen, behind which there is a posterior angular foramen, a large perforation not usually developed in other labyrinthodonts.

In mesial aspect the symphyseal region has a roughened area around its anterior margin,

presumably for the attachment of ligaments which held the two jaw rami together. A further large area of ligamentous attachment is provided by the highly irregular, much pitted buttress for the second parasymphysial tusk. Between and ventral to the two pitted areas is a cartilage-finished surface, extending from the dentary, where it surrounds the base of the more anterior tusk, onto the front of the splenial. Thus the structure of the symphysis suggests that slight movement of the jaw rami relative to one another was possible.

Behind the symphysis a shagreen of denticles extends backwards over the surface of the coronoids and onto the prearticular, around the lip of the adductor fossa. Teeth are borne only on the dentary, there being no enlargement of the coronoid denticles as occurs in some other temnospondyls. Details of dentition are discussed in a separate section.

Watson's outline of the jaw of *Megalocephalus* ('*Orthosaurus*' 1926), was based upon a virtually complete ramus from the Newsham Low Main Seam, the suture pattern being compiled from a large number of specimens from this horizon. A further jaw ramus, from the Airdrie Blackband Ironstone, is excellently preserved and largely confirms the previous composite lateral reconstruction. No single specimen shows a complete mesial surface, which is here reconstructed largely from four specimens, G15.29, G15.40, G15.43, G15.46, all from Newsham.

The lower jaw of *Megalocephalus* has all the bones which are characteristic of the labyrinthodont mandible (Nilsson 1944). The dentary is the tooth-bearing element, extending from the jaw symphysis of which it forms the major area, to the front of the adductor fossa, with its greatest exposure in lateral aspect. Viewed dorsally, a horizontal shelf of bone expands out behind the symphyseal region, but varies in width according to tooth size. This thickened alveolar area is triangular in section, with the apex pointing down. A thin wall of bone sheaths the bases of the teeth laterally. There is little mesial exposure of the dentary behind the symphyseal region since the three coronoid bones lie immediately below the tooth-bearing shelf.

The coronoids are elongate elements which bear a band of denticles. The anterior coronoid is a narrow strip of bone between the dentary and splenial, which tapers somewhat at the front since it extends well forwards towards the symphyseal region. The middle and posterior coronoids are roughly rectangular elements, although the posterior margin of the latter is indented by the adductor fossa. A small finger-like posterior process of the coronoid extends in a groove on the mesial surface of the surangular just ventral to the dentary tooth row. Contact with the surangular is weak, however, and the process is not visible in lateral aspect, unlike the condition in later temnospondyls where there is a trend towards increased size of this process which gains a broad sutural contact with the surangular and forms a high crest, visible on the external surface of the jaw.

The Meckelian space is floored by the two splenial bones and the angular since these elements have a lateral as well as a mesial exposure. Laterally sutures between the bones are more or less parallel and lie at an oblique angle to the posterior margin of the dentary bone. Mesially the splenial has a narrow anterior extension into the symphyseal area. It increases in depth towards the back of the parasymphysial tusk pair, beyond which point it extends mesially to form a ledge of bone of approximately 3 cm in length, which gradually tapers off posteriorly. The remainder of the bone lies in the vertical plane and contacts the prearticular and postsplenial along its posterior margins.

The postsplenial is, in mesial exposure, a narrow strip of bone preserved fully only in H.M. G15.40 and not recognized by Watson in his 1912 description. Along most of its length it

contacts the prearticular and posteriorly sutures with the angular bone, the posterior Meckelian fenestra lying in the normal labyrinthodont position between these two elements.

The angular and surangular together form most of the lateral surface of the posterior part of the jaw ramus. Only the angular, however, wraps around the hind edge of the ramus to present a relatively broad exposure on the mesial surface, where it has an extensive suture with part of the posterior margin of the pre-articular.

The posterior suture of the surangular with the articular apparently passes down, following the line of the posterior margin of the jaw. The area behind the lateral line groove lacks ornament and probably represents an area of insertion for the depressor mandibuli muscles, which must have extended onto the bones of the mesial surface. The surangular sheaths the lateral wall of the glenoid fossa and extends forward, its dorsal margin forming the lip of the adductor fossa. This region too lacks ornament, suggesting that slips of the adductor musculature were anchored here, while the main muscle mass passed through the fossa to insert on the inner surface of the surangular and angular bones. The comparatively large surangular ossification is apparently a primitive feature (Säve-Söderburgh 1936), since in later temnospondyls the angular extends upwards to occupy much of this original area.

The mesial wall of the fossa is formed mainly from the pre-articular, a long narrow element which fills a large area of the inner surface of the jaw. The posterior margin of the bone is not well preserved in any specimen, but presumably contacted the articular. Ventrally it sutures with angular and postsplenic elements. It tapers considerably in the anterior region and has a short contact with the splenic on a level with the mid-point of the middle coronoid. Dorsally it sutures with the posterior part of the coronoid series and forms the lip of the adductor fossa, an extension of the coronoid denticles forming a narrow band around this region.

The remaining lower jaw element is the articular, which represents the only ossification of Meckel's cartilage. It forms a massive buttress embraced laterally by the surangular. The shape of the fossa, when viewed dorsally, mirrors that of the quadrate condyle and may be divided roughly into two regions. The main horizontal articular surface has its long axis running transversely. A further articular face is directed antero-mesially and has a slight downward inclination. Since the adductor fossa has been closed up by compression during preservation of H.M. G15.26, the only specimen with a well preserved articular, the anterior limit of the ossification is not known. Also there is no knowledge of the foramen for the chorda tympani (mandibular) branch of the seventh cranial nerve, which in most Amphibia pierces the mandible just below the glenoid fossa. Again, because of post-mortem compression the critical region is not apparent.

Dentition

The dental formula for *Megalocephalus*, as applied by Chase (1963), is palate 2-2-2, pmx 8 or 9, mx 36. Thus the palate shows the generalized and seemingly primitive temnospondyl condition: a large labyrinthodont tusk and replacement pit are borne on a raised buttress on vomers, palatines and ectopterygoids. Where known, tusk length is approximately 30 mm and the basal diameter *ca.* 14 mm.

Although Chase notes the presence of 'canine peaks', i.e. enlarged teeth in the anterior part of the maxilla, in *Megalocephalus* there is no pronounced peaking such as occurs in some anthracosaur skulls. Instead there is general diminution in alveolar size from the front to the back of

the skull. The largest marginal teeth have a basal diameter of approximately 10 mm and the smallest 2 mm. The size grade is however interrupted since the ventral alveolar shelf narrows in the narial region and two relatively small teeth occur at the back of the premaxilla.

In labyrinthodonts it is usual for the dentary teeth to mirror the marginal dentition of the upper jaw, but in *Megalocephalus* the count for the lower dentition is considerably less than that of the upper jaw teeth. The estimated maximum lower tooth count is 34. The number is low since there is enlargement of some dentary teeth. There are three pronounced tusk pairs comparable to the palatal tusks in size and alternating with them in position (figure 15).

Thus when occlusion is considered, the small dentary teeth would lie in the groove between the maxilla and lateral palatal elements, mesial to the marginal teeth of the upper jaw. In occlusion the large dentary tusk pairs lie between the palatal tusk pairs completing the series.

The parasymphysial tusks of the dentary, a highly characteristic feature of the Family Loxommatidae, in *Megalocephalus* lie inside the anterior palatal fenestra when the jaws are closed and their tips may pierce the dermal roofing bones. The tips of the vomerine tusks, on the other hand, must have fitted alongside the small marginal dentary teeth immediately behind the parasymphysial tusk pair. Those of the second lower tusk pair extended between the vomer and palatine tusks and small craters for their reception are apparent on the lateral wall of the choana. Similarly the third dentary tusks would have extended up to fill the gap between the palatine and ectopterygoid tusks when the jaws were closed.

It was noted above that in some specimens of the Newsham population of *Megalocephalus* elongate parasymphysial dentary tusks had perforated the snout, whilst in others the skull roof was solid in this region. The sample is so small that no definite conclusions can be drawn on the significance of this feature. It is possible that it develops in some individuals with age, as appears to be the case in Crocodilia (personal study of British Museum (N.H.) material), but it is perhaps worthy of note that elongation of anterior teeth is a sexually dimorphic feature among members of both major lissamphibian Orders (Noble 1931). Perhaps the closest parallel is with the anuran *Dimorphognathus africanus* in which the male develops elongate pseudoteeth in the lower jaw symphysis, the position of exceptionally elongate tusks in some *Megalocephalus* skulls. Tooth elongation is also characteristic of many plethodontid salamanders and in *Hydromantes* and *Eurycea* the male develops long premaxillary teeth, which are used to stimulate the female during courtship.

Olsen (1969) reviewed the subject of sexual dimorphism among fossil amphibians and reptiles, where differences between sexes may involve distinct structural features or may be size dependent. Skull variation in *Megalocephalus* is probably of the second category. Of the two most complete Newsham skulls, H.M. G15.21 has a relatively short premaxilla with eight teeth and has no perforations through the snout for dentary tusks. H.M. G15.22 on the other hand is larger and considerably more robust with a proportionately broader, longer premaxilla which bears nine teeth. On the premaxillary-internasal boundary is a perforation on each side for parasymphysial dentary tusks, which were presumably more elongate than in the other skull. Similar variation can be seen in other more fragmentary Newsham material and it is possible that the two skull types may relate to sex differences.

Similarly, two distinct types of skull differing in proportion, robustness and in tooth size are described for *Seymouria baylorensis* (Vaughn 1966). In this species the population sample is sufficiently large to make the suggestion of sexual dimorphism credible, whilst in *Megalocephalus*, although it is interesting to speculate, the sample is inadequate to authenticate the suggestion.

The shape of loxommatid teeth is highly characteristic and they are quite distinct from those of contemporary anthracosaurs. The teeth of *Megalocephalus* (Embleton & Atthey 1874, pl. IV 'Loxomma allmanni') are lanceolate. In section they are circular at their base and for the first quarter of their length, thereafter becoming laterally compressed. The anterior and posterior edges form a sharp blade, continuous over the apical point. Tusks and teeth are of similar form. All are ridged longitudinally, particularly around their base.

Teeth vary considerably amongst contemporary anthracosaur genera (Panchen 1970). They may be slightly lanceolate, but where this occurs lateral compression is confined to the apical region, whereas loxommatid teeth are laterally compressed down most of their length.

The internal structure of Coal Measure labyrinthodont teeth has been studied by Embleton & Atthey (1874, 'Loxomma'; 1876, 'Anthracosaurus') and Schultze (1969) and it is possible to distinguish between loxommatid and anthracosaur by comparing histological detail. In the loxommatid the radial infolding of the external primary dentine shows a short branch at each angle, whereas the anthracosaur infolding, although more tortuous, always appear as single lines. This type of infolding is probably characteristic of all anthracosaurs (Panchen 1970).

A tooth section resembling that of *Megalocephalus* is figured by Dawson (1863) for *Baphetes planiceps*. Teeth of this type can also be observed in *Baphetes kirkbyi* (G.S. 28316) and in the holotype skull of *Loxomma acutirhinus* and they may well be common to all loxommatids.

MEGALOCEPHALUS LINEOLATUS (COPE 1877)

Comb. Baird (1957, p. 1693)

Specific diagnosis. Loxommatids of the genus *Megalocephalus* with a short cheek region, the quadrates lying just behind the level of the occiput. Tabular with slight posterior extension. No evidence of peaking along the dentary tooth row.

Distribution. Middle Pennsylvanian of North America.

Watson in 1926 was first to comment on the presence of a loxommatid in the fauna from the Upper Freeport Coal, Linton, Ohio, and includes *Leptophractus lineolatus* among synonyms for *Megalocephalus* ('*Orthosaurus*') *pachycephalus*.

In 1929 Watson attributed further material from Linton to the genus *Megalocephalus*. This included isolated teeth described by Newberry (1856) as *Rhizodus lancifer*, later ascribed to *Anthracosaurus* (Romer 1963; Panchen 1970) but now considered indeterminate (Panchen 1977), and also 'fragmentary maxillae and mandibles described by Cope as *Leptophractus obsoletus*'. The type material of *L. obsoletus* has however now been referred by Panchen (1970) to the Anthracosauria, since 'the dentition is probably eogyrinid with some degree of canine peaking'.

A further specimen B.M.(N.H.) R2676, this time undoubtedly loxommatid, was cited by Watson. He states: 'It is probable that the loxommatid which occurs in the fish-bearing canal at Linton, Ohio, is identical with *Orthosaurus*'. Romer however, in 1930 erected a further loxommatid genus – *Macrerpeton* – from the Linton material and in 1947 stated that all Linton loxommatids could possibly be assigned to this form.

Description of *Macrerpeton huxleyi* was based primarily on two skulls, the type of which later proved to be a normal edopoid and thus the genus *Macrerpeton* was removed from the Loxommatodea and assigned to the Edopoidea (Romer 1966). The second skull, although unmistakably loxommatid, is distinct from specimens of *Megalocephalus* in a number of features and is here assigned to the genus *Baphetes*. The only other specimen synonymized by Romer (1930) with

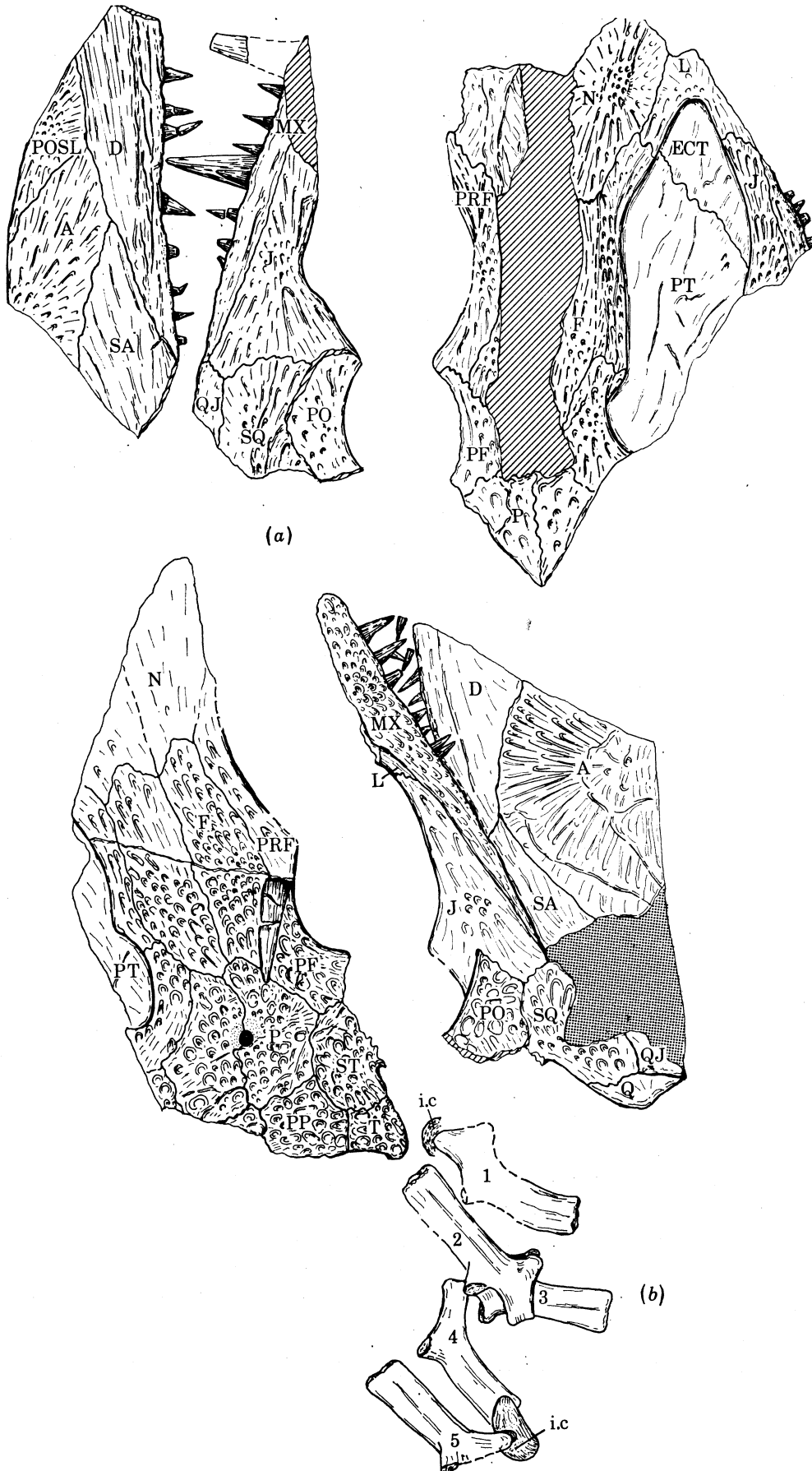


FIGURE 16. *Megalocephalus lineolatus* (Cope). Two-thirds natural size. (a) Holotype A.M.N.H. 6828 (preserved as a natural cast). (b) Plesiotype M.C.2.2162. Composite from original natural casts. The vertebrae are drawn from the right side of the specimen, while the skull table, which is preserved folded under the lower jaw, is drawn in approximate orientation.

Macrerpeton that may possibly be loxommatid is *Leptophractus dentatus* Moodie, an isolated dentary.

Baird (1957) described a further loxommatid specimen from Linton (figure 16*b*). The skull diagonistically that of *Megalocephalus* was, together with the type of '*Leptophractus*' *lineolatus* (figure 16*a*), assigned to the species *Megalocephalus lineolatus* (Cope 1877). Baird's specimen is of particular significance since it finally established the 'non-embolomeric' nature of loxommatid vertebrae.

Description of material

Holotype. A.M.N.H. 6826. Middle portion of skull and part of left mandibular ramus, described by Cope (1877) as *Leptophractus lineolatus*, preserved as natural cast. From Cannel below upper Freeport Coal, Diamond Mine, Linton, Jefferson Co., Ohio, U.S.A. Allegheny Series Middle Pennsylvanian (corresponding with Westphalian D of Europe) (Francis & Woodland 1964).

Other specimens attributed to this species. All from type horizon locality.

M.C.Z. 2162. Posterior part of skull with five associated vertebrae, preserved as natural cast.

B.M.(N.H.) R2675. Part of the right side of a skull, from the front of the antorbital vacuity to the naris, preserved as natural cast.

A.M.N.H. 6946. Dentary, described by Moodie (1916) as *Leptophractus dentatus*.

When Baird proposed specific separation of American material of *Megalocephalus* he suggested no features upon which specific diagnosis could be based. Since the two forms are geographically and stratigraphically distinct, taxonomic separation is reasonable. It is, however, difficult to find many morphological differences upon which this can be based for two reasons. Firstly, the paucity of American material – only three incomplete skulls can be assigned with certainty to *Megalocephalus*. Secondly, the relatively small size of the two more complete specimens makes comparison with *M. pachycephalus* difficult, since many of the apparent differences may be attributed to growth phenomena.

The British Museum specimen B.M.(N.H.) R2675 represents part of a skull of approximately the same size as a topotype H.M. G15.21 of *M. pachycephalus*. The snout is fractionally shorter but otherwise this region is similar in all respects to the British species. The other two specimens are from smaller skulls, of which the midline length is estimated at approximately 200 mm. Some of the bones, particularly nasal, lachrymal, jugal and lower jaw elements display a 'cobweb pattern' or ornament away from the centre of ossification, indicating incomplete growth of these regions (Bystrow 1935).

Measurements of various parameters indicates that the 200 mm skull possessed a relatively shorter snout, broader interorbital region and a considerably shorter cheek region, when compared to *M. pachycephalus*. While the first two characters may well be accounted for by the relatively smaller size of the skulls, the cheek region is almost certainly of taxonomic importance. When reconstructed from M.C.Z. 2162 the quadrate apparently lies just behind the back of the skull table, whereas *M. pachycephalus* has a very long cheek region. Studies of other labyrinthodont growth stages (Romer 1939; Dr A. R. Milner, private communication) indicate that such a drastic change in the proportions of the back of the skull would be exceptional at such a late stage (i.e. between 200 and 300 mm).

There is a single growth stage attributed to *M. pachycephalus* from the Irish Coal fauna,

B.M.(N.H.) R8465. This small skull measures only 40 mm midline length, but already has a long cheek region with the quadrate lying well behind the occipital condyle. Thus, if identification is correct, skull shape is largely determined at an early stage.

GENUS *BAPHETES* OWEN

Generic diagnosis. Loxommatids with a broad flat snout and parabolic skull outline. Pre-orbital region approximately half midline length. Antorbital vacuity slightly larger than orbit. Premaxilla short antero-posteriorly, bearing 10 or 11 teeth where known. Lachrymal reaches nostril. Skull table relatively large and square. Intertemporal bone present. Jugal may enter skull margin. Palate without anterior vacuity.

BAPHETES PLANICEPS OWEN 1854

The holotype of *Baphetes planiceps* from Nova Scotia was the first discovery of a loxommatid specimen. It is unfortunate that this fragmentary and incomplete skull is the only genotype skull material since, although it is obviously distinct from *Megalocephalus* and *Spathicephalus*, there is virtually no overlap with the posterior skull area preserved in the genotype specimen of *Loxomma*. A diagnosis distinguishing these two genera must ultimately depend upon material of species other than the genotype.

Watson (1929) attributed two specimens from the British Coal Measures to Owen's genus *Baphetes* on the basis of snout shape and structure, which is virtually identical to that of *B. planiceps*. In this and in a number of other features the British skulls are quite distinct from *Loxomma* and it is on these specimens that a generic diagnosis has been based.

Since, owing to the paucity of material, it is not possible to give an adequate specific diagnosis of *B. planiceps*, Watson deemed it unwise to attribute any further specimens to it and on the grounds of geographical separation erected new species for the British material (i.e. *B. kirkbyi*, see below).

Description of material

Holotype. B.M.(N.H.) R4056. Anterior part of skull sheared into two blocks, the ventral skull roof figured by Owen (1854, pl. IX) and the dorsal palate, together with numerous associated skull fragments. Also R.M. 3065, further fragments including tooth sections figured by Dawson (1863, pl. II). From the Albion Mine, Stellarton, Pictou County, Nova Scotia. Albion member of Division II, Stellarton Group, Lower Alleghenian, North America (Bell 1940) (corresponding to *Phillipsii* zone, Westphalian C of Europe).

The skull specimen, B.M.(N.H.) R4056, was discovered by Dawson in 1851 in a nodule of carbonaceous shale. Splitting of the nodule sheared the skull in a horizontal plane and exposed the ventral surface of the skull roof and the dorsal palatal surface (figure 17). Between the skull roof and palate had been a thin layer of matrix, some of which remains, particularly around the choanal region, but most of which has shattered out taking fragments of the bone surface with it. Owen's original description of this species (1854) was based solely upon the skull roof block. Subsequently the palate and other fragments also came into his possession and were the subject of a further brief description (Owen 1855).

No further preparation of the skull material has been possible, owing to its fragmentary

nature, but the layer of matrix from the orbital region can be fitted onto the specimen and this gives the outline and the relative position of the posterior margin of the orbit. Sutures are generally apparent and where known, skull roof structure is essentially similar to that of *B. kirkyi* (figure 21).

The anterior palate is of primitive loxommatid structure, with no vacuity. The relatively broad, rounded snout of *Baphetes* is correlated with a higher premaxillary tooth count than is recorded for either *Loxomma* or *Megalocephalus*. Ten teeth are apparent on the premaxilla,

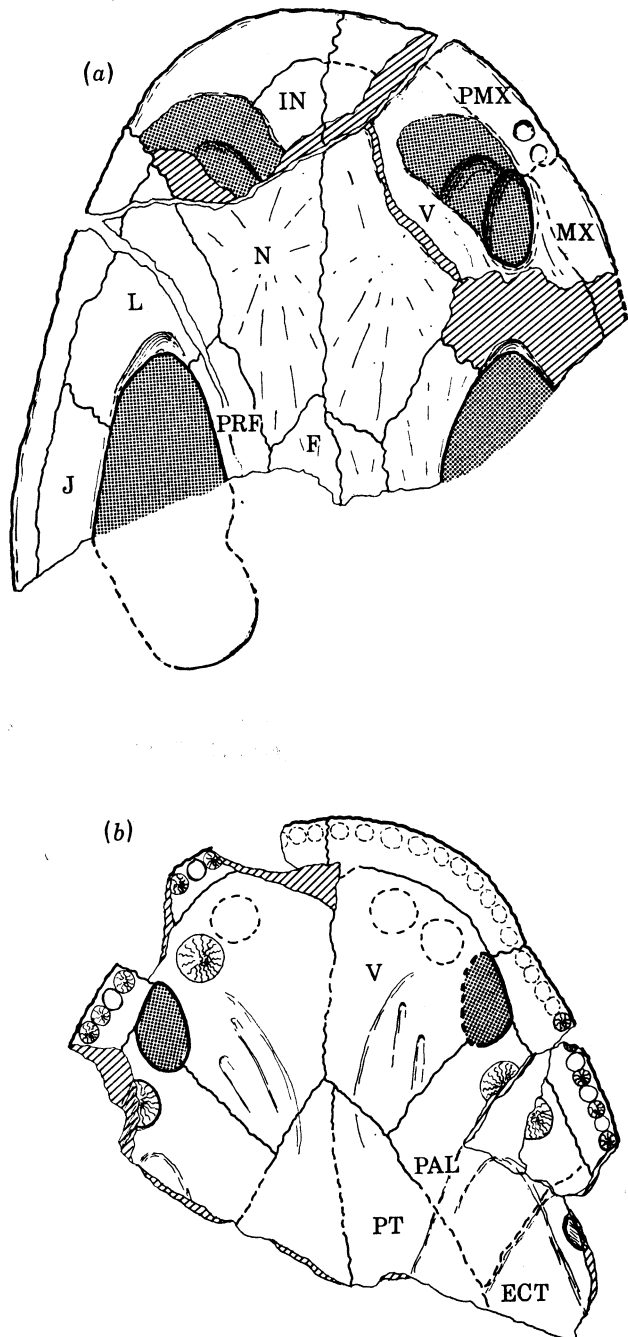


FIGURE 17. *Baphetes planiceps* Owen, holotype skull. Half natural size: (a) Ventral surface of skull roof with the posterior margin of the right orbit added from matrix impression, (b) dorsal surface of palate.

whilst approximately 12 maxillary teeth occur anterior to the level of the first ectopterygoid tusk. Where known the marginal teeth are of a uniform size, with a base-crown length of approximately 1 cm. The paired palatal tusks can be examined mainly as planed down basal transverse sections, or as longitudinal sections through the broken edges of bone. A vomerine tusk is preserved undamaged, and is slightly recurved, being some 2 cm long with a basal diameter of 1 cm. Dawson (1863) figures a tooth section in a transverse plane. Its structure is comparable with that described for *Megalocephalus* (Schultze 1969) and *Loxomma*.

The choanae, which are ovoid and slightly elongate, are apparent on the dorsal palatal surface and in outline on the area of matrix adhering to the skull roof. A shallow rounded groove mesial to the choana appears in part on both blocks and in the sheet of matrix which fits between them. It extends from the left choana to the interorbital region. This depression of the dorsal palatal surface may indicate the mesial wall of a large nasal capsule, extending down the middle of the vomer and onto the anterior region of the pterygoid. The dimensions of the structure, taken from the outline on the area of matrix from this region, indicate an overall length of some 6 cm, with a maximum width of 3 cm across the choana, gradually narrowing to 1.5 cm at the level of the tip of the antorbital vacuity, near its posterior limit in this interorbital region. Such a structure corresponds in outline to that indicated for *Megalocephalus*.

Also on the dorsal surface of the palate are two pairs of deep grooves, which run parallel to one another and lateral to the supposed mesial wall of the nasal capsule. These pierce the surface of the vomer as it thickens around the margin of the choana. The foramina so formed may carry branches of the profundus and olfactory nerves respectively.

BAPHETES KIRKBYI WATSON 1929

(= *Baphetes latirostris* Watson)

Specific diagnosis. Loxommatids of genus *Baphetes* with jugal entering into skull margin, preventing contact between maxilla and quadratojugal. Supratemporal extending around apex of otic notch. Skull attaining large size; known midline length (front of snout to back of skull table) up to 290 mm.

Distribution. Middle and base of Upper Coal Measures (Westphalian B, C), Britain.

Description of material

Holotype. Skull collected by J. W. Kirkby, represented in part by natural cast.

H.M. G15.69. Impression of dorsal surface of right side of skull.

H.M. G15.70. Impression of palate (incomplete in midregion).

H.M. G15.91. Skull table and basicranial region.

From Pirnie Colliery, East Fifeshire, Scotland. Earl David's Parrot Coal, Modiolaris zone, Middle Coal Measures (L. Westphalian B) (Panchen & Walker 1961).

Attributed specimens. G.S. 28316, anterior part of skull with counterpart, described by Watson (1929) as *Baphetes latirostris* from Airdrie or 'Mushet's' Blackband Ironstone, near Airdrie Lanarkshire, Scotland: U. Modiolaris zone, Middle Coal Measures (Westphalian B) (Westoll 1951; Panchen & Walker 1961).

B.M.(N.H.) R2753, part of a skull table with associated braincase and B.M.(N.H.) R2755, left premaxilla, possibly from the same skull. From Bradford Coal Group, Manchester, Lancashire. U. Phillipsii zone, Upper Coal Measures (Westphalian C) (Tonks *et al.* 1931).

Watson (1929) referred two British skulls to Owens's genus *Baphetes* on the basis of similarity in snout shape and structure. He erected two separate species for this material, basing his distinction upon the size of the naris and the presence of a single or paired internasal ossicles.

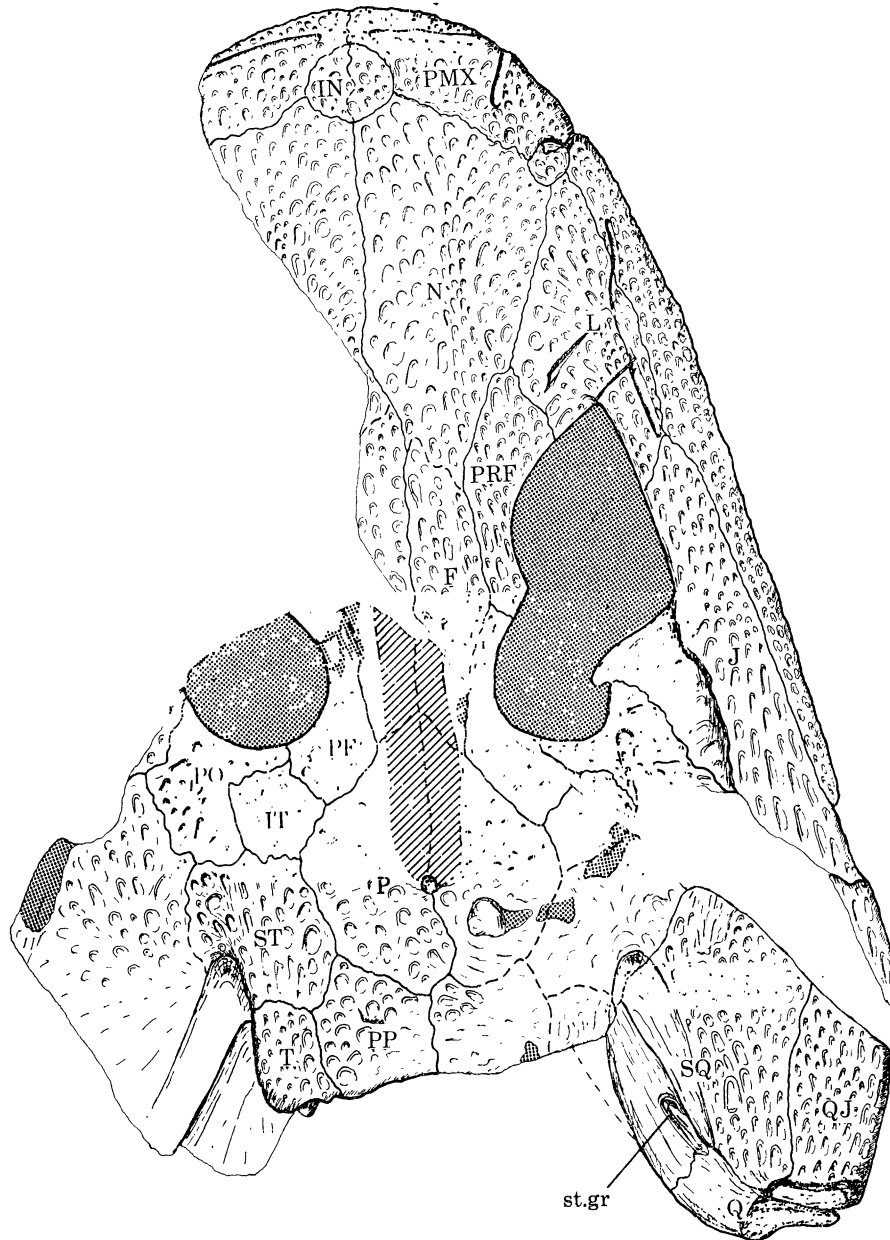


FIGURE 18. *Baphetes kirkbyi* Watson, holotype skull in dorsal view. Half natural size. Only the region of the skull table is preserved and thus the right side is drawn from a latex cast of the upper block.

The latter feature is found to vary among individuals of *Megaloccephalus pachycephalus* and since part of a median suture can be traced across the region of the internasal in the holotype of *B. kirkbyi*, ossification must have proceeded from two centres in this skull too. Differences in the narial region would appear to be the result of preservation rather than marked structural distinction. In the holotype of *B. kirkbyi* the septomaxilla, a small loose element, appears to

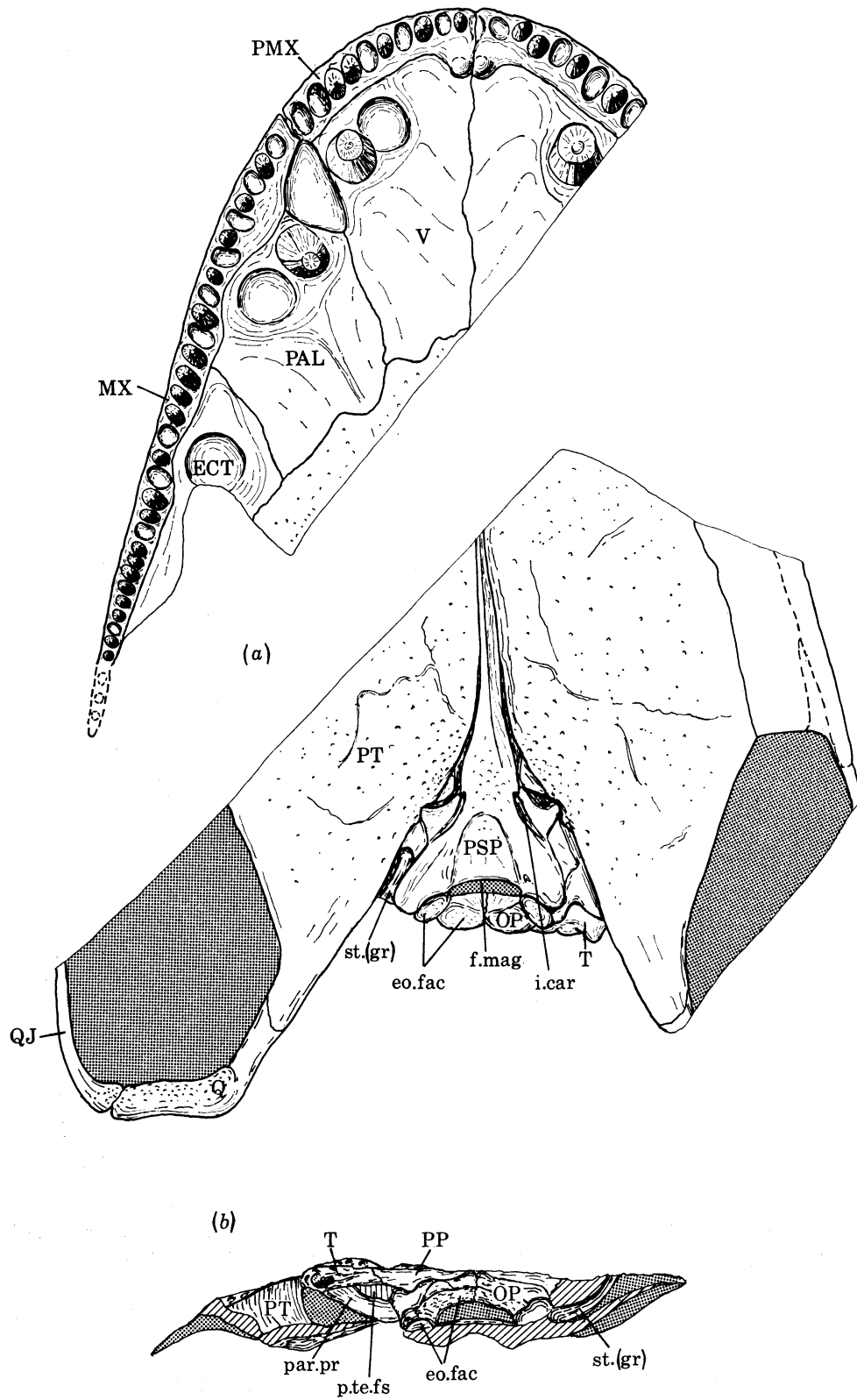


FIGURE 19. *Baphetes kirkbyi* Watson, holotype skull. Half natural size: (a) palatal view, from a latex cast of the lower block with detail added in the region of the braincase, which is preserved; (b) occiput.

fill virtually the whole narial opening. This is most likely due to distortion during preservation since there is a distinct ridge along the mesial and posterior borders of the right premaxilla where the element has been pushed back across the margins of internasal and nasal bones. The shift has also resulted in a slight closing of the naris, which presumably was of essentially the same structure as in the Airdrie skull. The apparent difference in width of the anterior region of the maxilla in the two specimens of *B. kirkbyi* is again largely due to difference in preservation. The Airdrie skull has suffered considerable dorso-ventral compression which has

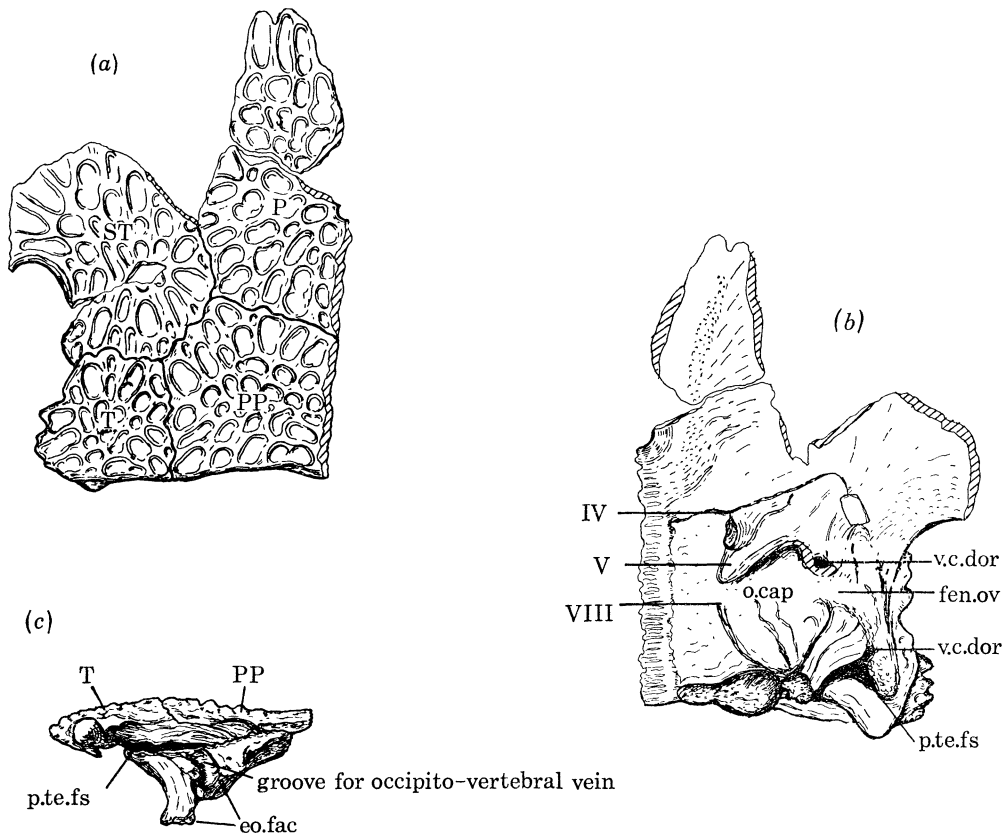


FIGURE 20. *Baphetes kirkbyi* Watson, B.M.(N.H.) R2753. Natural size: (a) dorsal, (b) ventral, (c) occipital view.

splayed the maxillae out, whereas in the holotype they retain a more normal curvature. Apart from a slight difference in size there are no significant differences between the two skulls and both have been referred here to the species *B. kirkbyi* Watson, which takes priority over his species *B. latirostris*.

Although from different horizons, both Watson's skulls are from the Modiolaris zone (Westphalian B) of Scotland. From a higher horizon to either of these, but also considered to be conspecific, are two fragments of a further skull of *Baphetes*. The specimens B.M.(N.H.) R2753, R2755 are from the Bradford Coals, Manchester, which lie near the top of the Phillipsii zone (Westphalia C) and as such represent the last known occurrence of a labyrinthodont in the British Coal Measures.

Dermal skull roof

Reconstruction of the skull roof (figure 21) is based largely on the holotype skull (figure 18). The snout and right cheek region are represented by sharp impressions on the shale matrix, the bone having rotted out, and were therefore studied from latex casts. Only the skull table area is represented by bone, the surface of which was completely cleared of matrix so that the sutures could be mapped.

The skull is essentially parabolic in outline with a broad, flattened snout, large, square skull table and long, deep cheek region. The nares lie near the jaw margin and less far removed

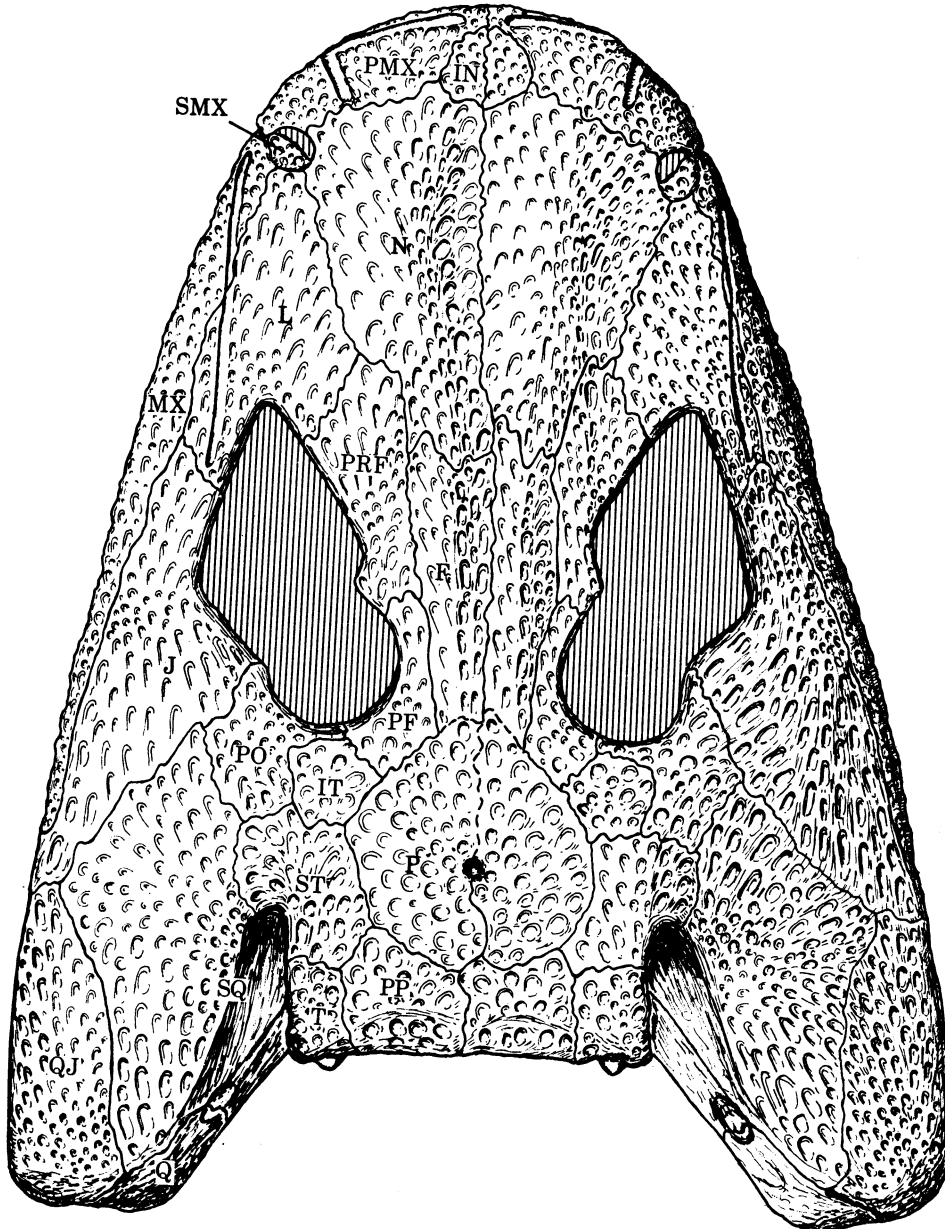


FIGURE 21. *Baphetes kirkbyi* Watson, composite restoration of the skull in dorsal view. Half natural size.

from the tip of the snout than in *Loxomma*, related to a difference in premaxillary shape. The antorbital vacuity is slightly larger than the orbit proper, the resultant fenestration being longer than in *Loxomma*, but less elongate than in *Megalocephalus*. The pineal foramen is relatively small (4 mm) and flush with the general skull surface. The ratio of skull width at the nares to that across the quadratojugals is 1:2, in contrast with that of 1:3 for the more acutely triangular skulls of *Loxomma* and *Megalocephalus*. The holotype is a relatively large skull, midline length (premaxillae to postparietals) being 270 mm. The Manchester skull fragments have individual proportions that are marginally smaller than those of the type, while the Airdrie specimen is part of a somewhat larger skull, estimated at some 290 mm midline length. A further distinguishing feature of this species from both *Megalocephalus* and *Loxomma* is the relatively short maxilla, which is separated from contact with the quadratojugal by the jugal, which enters into the skull margin.

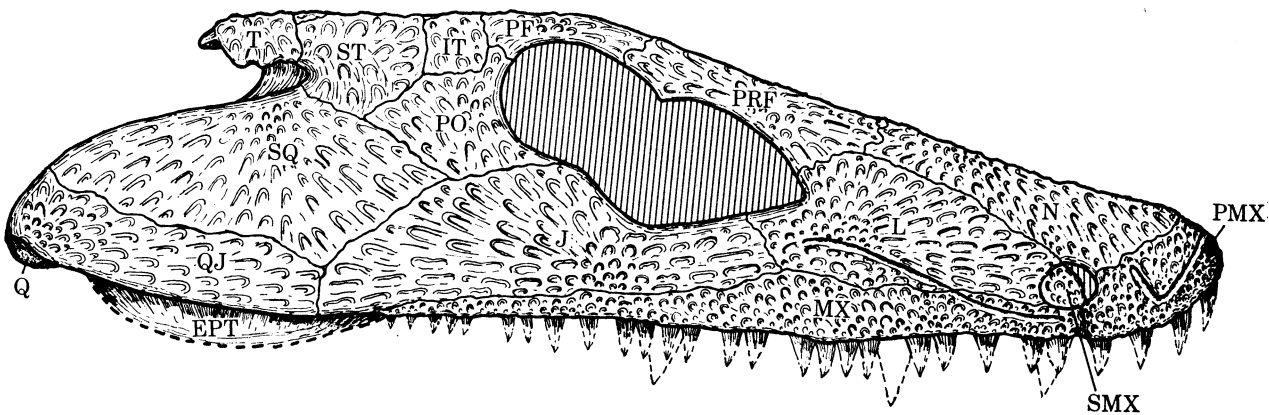


FIGURE 22. *Baphetes kirkbyi* Watson, composite restoration of the skull in lateral view. Half natural size.

Lateral line canals are only apparent on the anterior region of the skull and although following a similar course they are far less distinct than those of *Megalocephalus*, there being only slight deepening and extension of the dermal ornament rather than well-defined grooves. There is little trace of the suborbital canal on the Airdrie skull, but it is apparent in the holotype from the postero-lateral wing of the lachrymal, passing forwards before turning down onto the maxilla. The supra-orbital lateral line presumably followed the ridge along the midregion of the frontal and nasal bones but the only trace of the canal itself is on the premaxilla. Anteriorly the supra-orbital canals are joined by an ethmoid commissure, traces of which are apparent in all three specimens.

The most important feature that came to light from development of the holotype skull table was the presence of a large intertemporal ossification in the mesial part of Watson's postorbital (1929, figure 18). In the past any loxommatid with an intertemporal was attributed to *Loxomma*, whereas it now appears that some of this material may be more correctly referred to *Baphetes* on the shape of the snout.

The skull table is large and square, with long tabular and post-parietal bones. The posterior margin is incomplete in the holotype, but can be reconstructed from B.M.(N.H.) R2753 (figure 20), a beautifully preserved skull table fragment. Only the midregion anterior to the pineal foramen is missing in all three specimens. In the holotype this region is eroded down to the underlying sphenethmoid.

The supratemporal extends around the apex of the otic notch in this species but is more rectangular in other *Baphetes* skulls. A further characteristic feature of the skull table is the shape of the postorbital. In *Baphetes* the intertemporal has its antero-lateral corner extending into the postorbital, whereas in *Loxomma* the two bones meet in an oblique suture. Thus in this and other species of *Baphetes* the postorbital has a distinct finger-like process contacting the postfrontal.

Alignment of the skull table with the snout region shows that the holotype skull was somewhat asymmetrical, the right orbit lying on a level slightly behind that of the left. However, this has probably been accentuated by the compression force which has caused some infolding of the right lateral cheek region, whilst that of the left side has been folded out.

Palate

The palate of *B. kirkbyi* can be fully reconstructed (figure 23) from the holotype (figure 19) and the Airdrie specimen (Watson 1929, fig. 21). Although it is somewhat broader than that of *Loxomma*, it is of similar construction, being of the primitive closed type, lacking the anterior fenestration that is characteristic of *Megalocephalus*.

The premaxillae are distinct from those of other loxommatid genera in their relatively high tooth count. Both Scottish skulls have 10 premaxillary teeth, whilst the isolated premaxilla from the Manchester Coalfield has 11. In both skulls the maxillary tooth count is 34, less than in *M. pachycephalus* but higher than that estimated for *Loxomma*. The usual large palatal tusk pairs are present.

Braincase and parasphenoid

No composite restoration of the braincase of *Baphetes* has been attempted, since only the otic region is known. It is of characteristic loxommatid shape, although in this species the anterior 'wings' of pro-otic are less extensive than those described for other genera. Also the parasphenoid which sheaths it ventrally shows greater lateral expansion than either *Loxomma* or *Megalocephalus*.

An important feature, apparent in the holotype skull, is a median suture in the roof of the posterior region of the braincase (figure 19) confirming that this structure is formed posteriorly from paired opisthotic ossifications and that no median supraoccipital bone is present. The complex structure of the opisthotic is clearly apparent in the Manchester skull B.M.(N.H.) R2753. The relative levels of its two facets for columns of the exoccipital can be seen in occipital view (figure 20c) and the notch between the two facets indicates the probable place of emergence of cranial nerves IX, X and XI from the skull. Laterally the dorsal margin of the opisthotic forms the lower rim of the post-temporal fossa, a cavity which extends antero-mesially above the otic capsule. A perforation in the postero-lateral wall of the capsule indicates the probable point of emergence of the vena capitis dorsalis from the post-temporal fossa at the back of the skull. Also a deep groove, which extends dorsally from the area between the two opisthotic facets mesial to the supposed vagus foramen, towards the mesial extent of the post-temporal fenestration, may indicate the course of the occipito-vertebral vein.

Since the parasphenoid is missing in the Manchester specimen the roof of the otic capsule is seen in front of the facets for the exoccipital. From the supposed vagus foramen between the two facets, a ridge of bone sweeps forward dorso-medially and its anterior extremity marks an opening in the mesial wall of the otic capsule, presumably for the auditory nerve. A canal which

is assumed to mark the course of the fifth cranial nerve from the pro-otic foramen begins just in front of the auditory foramen and runs antero-laterally across the pro-otic wing.

Cranial nerve IV apparently emerged from the braincase in front of the pro-otic foramen in a similar position to that figured for *Palaeoherpeton* (Panchen 1964). Its course is marked by a smooth-sided groove in the dermal skull roof between the anterior limit of the otic region and the ridged attachment surface for the sphenethmoid.

The roof of the fenestra ovalis is apparent in the lateral wall of the otic capsule. A ridge of bone from the lateral facet for the exoccipital swings forwards dorsolaterally and forms the

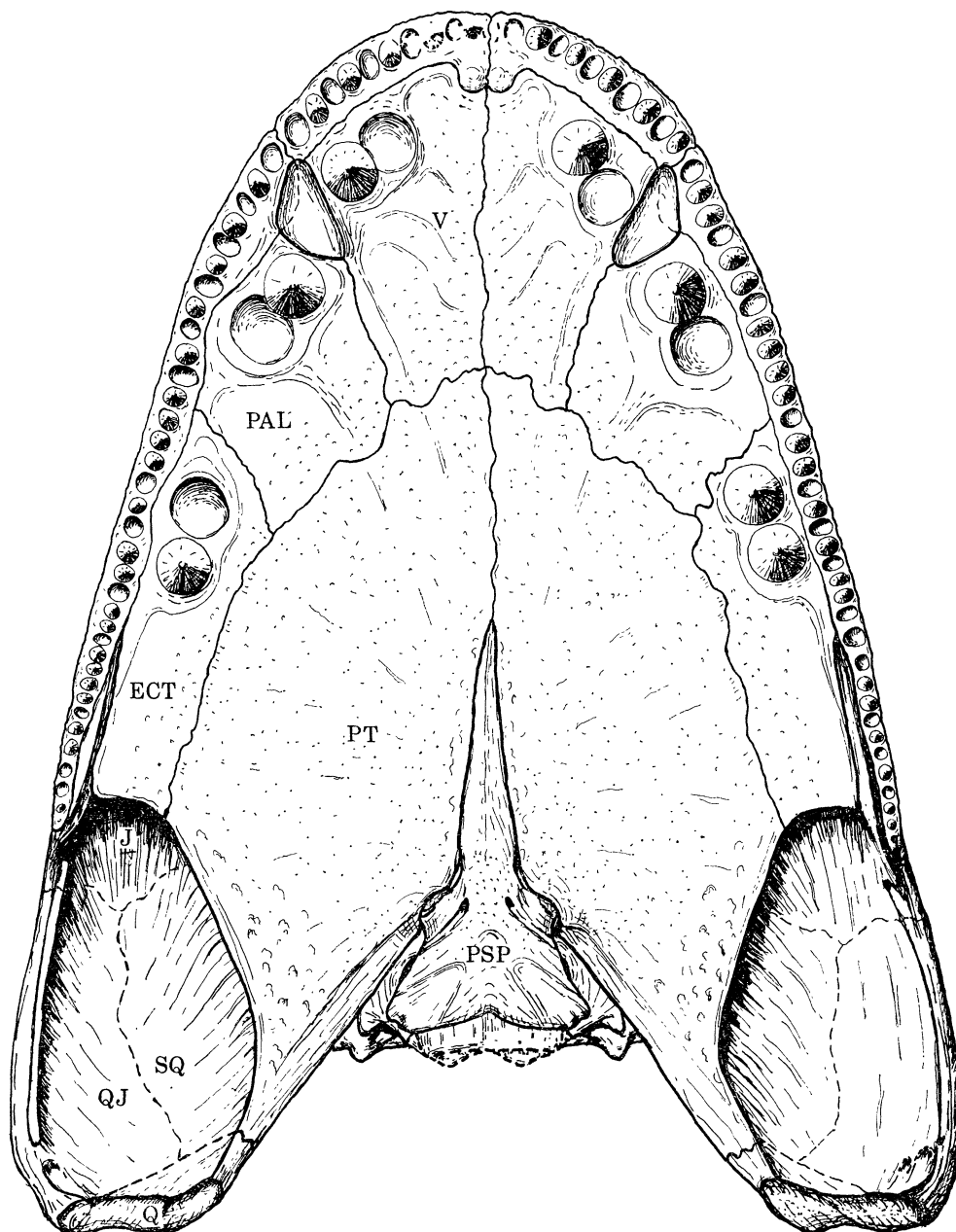


FIGURE 23. *Baphetes kirkbyi* Watson, composite restoration of the skull in palatal view. Half natural size.

posterior margin of the fenestra ovalis. As has been described for *Loxomma*, the floor of the fenestra would have been formed from the parasphenoid.

In front of the fenestra ovalis is a large foramen through the pro-otic which passes above the otic capsule into the post-temporal fossa and presumably marks the place of entry of the vena capitis dorsalis.

Watson (1929) comments on the condition of the stapes in the holotype skull of *B. kirkbyi*. The bone itself is not preserved but there is a clear impression of its position in H.M. G15.91. The groove indicates that the element was almost 2 cm long and extended from the fenestra ovalis dorso-laterally up to the otic notch. Apart from a triangular footplate preserved in the topotype (H.M. G15.21) of *Megalocephalus pachycephalus* there is no trace of this element in any other loxommatid.

BAPHETES LINTONENSIS SP. NOV.

Specific diagnosis. Loxommatids of the genus *Baphetes* in which the maxilla reaches the quadra-tojugal and excludes the jugal from the skull margin. Since the only specimen is a juvenile and differences may be size related, further diagnosis is not possible (see below).

Known distribution. M. Pennsylvanian, N. America.

The holotype specimen (A.M.N.H. 6944) was originally referred by Cope (1875) to the nectridean species *Sauroplorea newberryi*. However, with further development it became apparent that the specimen was loxommatid and Romer (1930) associated it with the larger type skull of *Macrerpeton (Tuditanus) huxleyi* (Cope 1875). His reconstruction of this species (1930, fig. 21) was a composite of both specimens and is described (Romer 1947) as a skull similar in almost every respect to that of *Loxomma* and *Baphetes*, but approaching the latter genus more closely and possibly cogenetic with it.

Later the holotype skull of *Macrerpeton huxleyi* was found to differ considerably from Romer's other specimen, since it lacked the antorbital fenestration peculiar to loxommatids. Thus the genus *Macrerpeton* was transferred to the Edopoidea (Romer 1966). However, the smaller skull is undoubtedly loxommatid and apparently cannot be referred to *Megalocephalus*, the other loxommatid genus that occurs in the Linton fauna. As was noted by Romer (1947) it closely resembles specimens of *Baphetes* and has been referred to this genus as a new species, *B. lintonensis*, the specific name being derived from that of the locality.

Description of material

Holotype. A.M.N.H. 6944. Skull and jaws, as natural casts. Described by Cope (1875, pl. 37, fig. 3) as *Sauroplorea newberryi* paratype and by Romer (1930, fig. 20) as *Macrerpeton huxleyi*. From Cannel below U. Freeport Coal, Linton Diamond Mine, Jefferson Co., Ohio, U.S.A. U. Allegheny Series, M. Pennsylvanian (corresponding to Westphalian D of Europe).

The following description is based on casts of the holotype, kindly supplied by Dr Donald Baird. No material other than the holotype skull can be referred with certainty to this species. Romer (1930) attributed a number of postcranial specimens to *Macrerpeton* but later (1947) referred them to *Colosteus*.

The skull is small (7.5 cm estimated midline length) and exposed from both dorsal and palatal surfaces and the lower jaw rami, each visible from their lateral surface, overlies much of the palate. The specimen has suffered considerable dorso-ventral compression, which has displaced

some of the elements and has pushed the mesial edge of the right pterygoid up through the skull roof. The snout region is incomplete and both quadrates together with the articular end of the left jaw ramus are missing, apparently having sheared off the block.

From the nature of the dermal ornament it is apparent that the skull is that of a juvenile animal. On the skull table the ornament has a typical pit and ridge structure but in other areas pitting is confined to the centre of each element and fine striations radiate from this point, a condition typical of a labyrinthodont growth stage (Bystrow 1935).

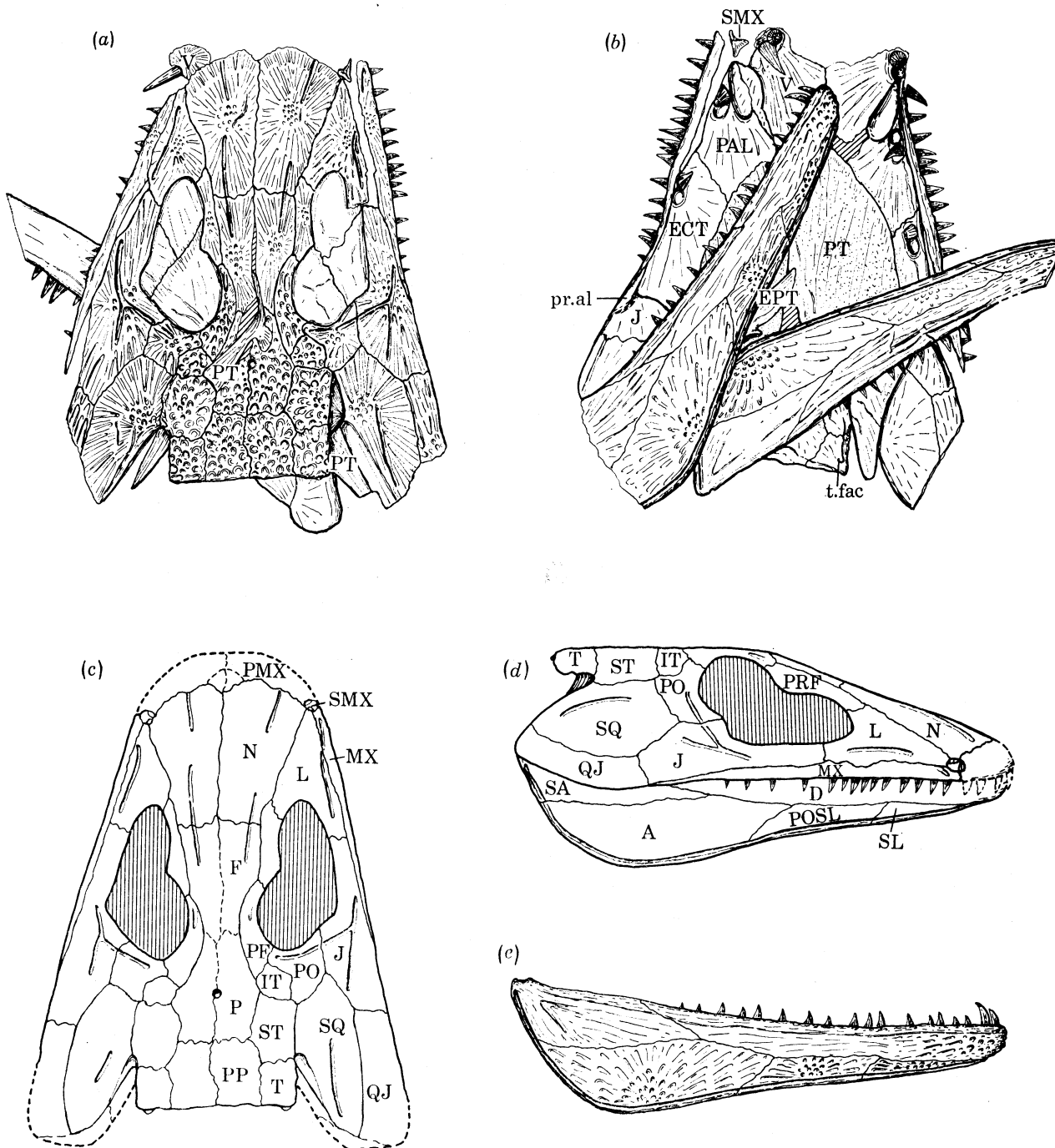


FIGURE 24. *Baphetes lintonensis* sp. nov., holotype skull. Natural size: (a) dorsal, (b) palatal view, (c) restoration of skull roof in dorsal view, (d) restoration of skull and jaws in lateral view, (e) restoration of right jaw ramus.

Dermal skull roof

Since the midregion of the palate lies horizontally in the skull, it has suffered little distortion from compression, and provides a reasonable datum for assessing the curvature of the skull roof in reconstruction (figures 24*c, d*). The total length of the skull is ascertained from the length of the jaw ramus, which indicates that there was a relatively short premaxilla, not a long triangular structure as occurs in *Loxomma*. The shape of the premaxillae is confirmed in part by the shape of the nasals. These extend anteriorly well in front of the level of the nares, in contrast to the condition in *Loxomma* or *Megalocephalus*. The shape of the antero-mesial border of the nasal indicates that a small internasal ossification was present as in other loxommatid species.

On the right side of the skull the maxilla has become detached from the lachrymal and pushed laterally, thus opening up the naris and isolating the small septomaxilla, which is visible both in dorsal and palatal view. This is the only loxommatid skull in which the structure of the septomaxilla is easily seen and it is similar to that described for *Edops* (Romer & Witter 1942). The dorsal exposure is essentially triangular with the apex extending to form an antero-laterally directed process, which on the palatal exposure projects ventrally and, were the bone correctly oriented, would contact the vomer. Such a palatal process, possibly homologous with the pars palatina of the lateral rostral (Panchen 1967), is also a feature of the septomaxilla of *Edops*, *Eryops* and possibly *Seymouria*.

The lachrymal contacts the septomaxilla and extends back to form the anterior margin of the antorbital vacuity. Thus the maxilla has no contact with the nasal and its width is relatively constant. The extent of the maxilla is however greater than that of *B. kirkbyi*, since it extends back to the level of the quadratojugal and excludes the jugal from the skull margin.

The skull table is relatively large and square with tabular and postparietals comparatively longer than in *Megalocephalus*, the other Linton loxommatid. A further distinguishing feature from the latter genus is the presence of an intertemporal bone. Romer (1930) notes that there may be an intertemporal present on both sides of this skull, but as the bone is absent in the type skull of *Macrerpeton* he figures its area as part of the postfrontal in his composite reconstruction. However, in *Megalocephalus* the corresponding area is occupied by a flange of supratemporal and in no loxommatid genus is the postfrontal comparable in shape with that of *Macrerpeton*. Using both sides of the skull all the sutures defining the intertemporal can be traced with certainty, indicating that its position corresponds exactly to that in other species of *Baphetes*. The shape of the intertemporal results in a postorbital of characteristic shape for *Baphetes*, with a mesial process contacting the postfrontal.

It is probable that the junction between the skull table and cheek region was still relatively kinetic. Their common boundary forms a straight line and has been pulled apart on the right side of the skull. Supratemporal shape is, however, likely to be a juvenile characteristic, since on the side of the skull this element has a slight lateral extension onto the cheek region. Presumably in the adult skull both supratemporals would have extended laterally, thus sealing the kinetism.

The lateral line canals of the skull roof are very strongly developed. This too may be due to the juvenile condition of the only known skull. There is no trace of the lateral line system on the skull table, where the pattern of dermal ornament is of the adult type (Bystrow 1935). The supra-orbital canal occurs on the postfrontal around the mesial margin of the orbit. It appears again as a deep groove crossing the fronto-nasal suture, and finally reappears as a groove

from the midregion of the nasal to its anterior margin, where it presumably extended forwards onto the premaxilla.

The infra-orbital canal can be traced from the postorbital onto the jugal where it joins with the jugal canal. It reappears on the lachrymal and a final section is situated near the anterior tip of the maxilla. The first part of the jugal canal is on the jugal and it reappears after a gap, near the mesial margin of the squamosal. Its continuation as the mandibular canal appears along the lower surface of the lower jaw.

Palate

Much of the palatal surface is overlain by the jaw rami. The anterior region, including the premaxillae and anterior part of the vomers, is missing and posteriorly the quadrate rami of pterygoid and epipterygoid have been disorientated into a more horizontal plane. The middle region of the palate is, however, relatively undistorted and well-preserved and it is evident that there was a simple closed palate, essentially similar in structure and proportions to that figured for *B. kirkbyi*. The maxillary tooth count is estimated at about 30.

On the left side of the skull the quadrate ramus of the pterygoid has been completely detached from the cheek region and has been pushed forward. Its mesial edge, which forms part of the conical recess, has been pushed up through the skull roof. On the right side of the skull the quadrate ramus of the pterygoid has been folded out with the cheek region during compression. This has apparently displaced the epipterygoid across the palate, and it now projects from beneath the lower jaw ramus.

As no part of the braincase is preserved in this skull it must either have fallen out prior to fossilization or have been unossified. Facets for its reception are apparent on the ventral surface of the skull table.

Lower jaw

The lower jaw is visible only in lateral aspect where its structure is essentially similar to that described for *Megalocephalus*. The main differences appear to lie in the dentition. Parasymphysial tusks occur in the anterior region of the dentary, but are proportionally smaller than those of *Megalocephalus*. Also there are no marked peaks in tooth size along the dentary tooth row of the kind which characterize *Megalocephalus*. The dentary tooth count for *B. lintonensis* is estimated at 35.

BAPHETES BOHEMICUS (FRITSCH 1889)

(= *Loxomma bohemicum* Fritsch)

Specific diagnosis. Loxommatids of the genus *Baphetes* with a relatively short, broad skull. Lateral line grooves well-developed on cheek and postorbital region.

Steen (1938) when reviewing the fauna of Nýřany noted that the labyrinthodont dentary, the only material of Fritsch's species *Loxomma bohemicum*, was unless identified with more complete material both generically and specifically indeterminate. She therefore referred to this species the only loxommatid skull identified in the fauna (C.G.H. 3509) and it is upon this specimen that her skull reconstruction of the species was based (1938, fig. 24).

At the time of Steen's description the presence of an intertemporal bone was, among loxommatids, believed to be diagnostic only of the genus *Loxomma*. This ossification is now known to be present also in *Baphetes*.

Skull shape in the Nýřany loxommatid is highly characteristic of the genus *Baphetes*. In addition the stratigraphic position favours inclusion of the species in the latter genus. The last record of *Loxomma* is in the Modiolaris zone (M. Westphalian B) of Britain, whereas *Baphetes* is known from the Upper Coal Measures of both Britain and North America. Thus, on the grounds of skull structure (described below) and horizon, it is proposed to transfer Fritsch's species to the genus *Baphetes*, as *B. bohemicus* Fritsch.

Description of material

Holotype. Anterior part of dentary and isolated teeth (figured Fritsch, Taf. 58, figs 3–9). From the Gaskohle, Nýřany (Nyran or Nürschan), Pilsen Basin, Bohemia, Czechoslovakia, Nýřany Series, Lower Grey Beds, Westphalian D (Němjec 1952).

Attributed specimens. Topotype C.G.H. 3509. Incomplete skull, exposed dorsally. Counterpart incorrectly figured by Broili (1908) as *Sclerocephalus credneri* Fritsch. Specimen attributed to *Loxomma bohemicum* by Steen (1938).

The skull (C.G.H. 3509) (figure 25a) has been studied from a latex cast, prepared by Dr Rădvan Hörny of the Narodni Museum. The specimen has suffered considerable dorso-ventral compression, which has folded out the cheek regions, opening up the otic notch on each side.

Many of the bones have become detached from the skull, which is incomplete along the margins of the snout and cheek region. One of the detached premaxillae is preserved on the block and is figured re-orientated at the front of the skull. Both maxillae are also preserved. The left has been pushed across the lateral cheek region and now obscures the shape of the antorbital vacuity. The right maxilla has been rotated antero-laterally and is partially overlain by part of a left pterygoid, possibly from the same individual. The region of pterygoid around the conical recess is preserved from the ventral surface, which bears the usual shagreen of denticles.

The right squamosal and jugal have been pushed antero-mesially, accentuating the natural asymmetry of the skull.

The skull roof has been reconstructed from the specimen (figure 25b). The isolated right premaxilla fits against the anterior border of the nasal completing the anterior snout and indicating a total midline length of some 18 cm.

A sheet of matrix covers the lateral border of the characteristically short premaxilla, but mesially it is complete and from its shape it is likely that small paired internasal ossicles were present.

The posterior margin of the external naris is preserved between lachrymal and nasal bones. The shape of the nasal bone, sweeping forwards to a level in front of the naris, is characteristic of *Baphetes*.

The left maxilla is apparently complete since it is of approximately the same length (11.8 cm) as its fellow, the posterior section of which forms a ridge along the overlying pterygoid. The tooth count is estimated at 30. When re-oriented from the narial region, it would appear from the line of the jugal-quadratojugal suture that the maxilla does not extend to contact the latter element, and thus it is assumed that the jugal enters the skull margin as in *B. kirkbyi*.

In her reconstruction of the skull roof Steen figures an extremely large irregularly-shaped antorbital vacuity, the lateral border of which was formed in part by the maxilla, which prevented the normal suture between jugal and lachrymal. The structure of this lateral region of

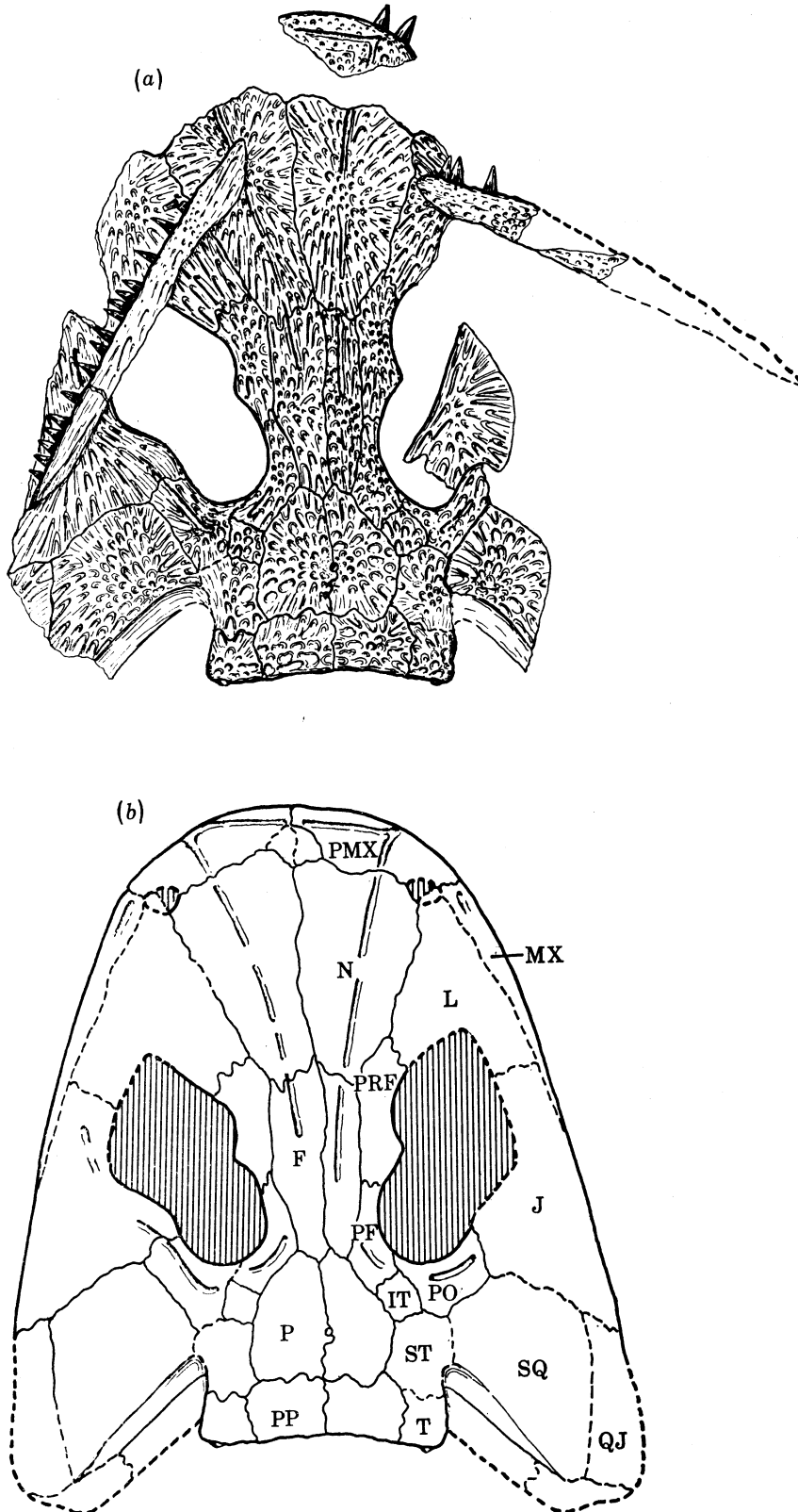


FIGURE 25. *Baphetes bohemicus* (Fritsch), topotype skull, (a) in dorsal view from latex cast, (b) restoration of skull roof. Half natural size.

the skull is not apparent on either side of the specimen, but since the teeth of the left maxilla appear to overlay ornamented dermal bone, it is assumed that the structure of the lateral cheek region is normal. The known extent of the orbit and antorbital vacuity agrees in shape with that of other species of *Baphetes* and there would seem to be justification for reconstructing the normal slipper-shaped vacuity.

As in other species of *Baphetes* the relatively large intertemporal allows only a short suture between postfrontal and postorbital, so that the latter extends mesially into a distinct finger-like process.

As in *B. lintonensis* traces of the lateral line system are more extensive than in most other loxommatid skulls. This feature, together with the comparatively short, broad shape of the skull may be indicative of some degree of neoteny in this species.

FUNCTIONAL MORPHOLOGY OF THE LOXOMMATID SKULL

The skulls of the three genera that comprise the family Loxommatidae differ in shape, but are essentially similar in basic construction, when it comes to consideration of their functional morphology. The presence of lateral lines, the long tooth row of sharp lanceolate marginal teeth, the large palatal and in *M. pachycephalus* dentary tusks indicate that they were aquatic piscivorous predators. Other aspects of their skull morphology show a high degree of specialization to this habit.

Whilst the external naris lies near the jaw margin, in the position assumed to be primitive for tetrapods (Panchen 1967), in the undistorted skull of *M. pachycephalus* it is largely occluded by the septomaxilla, which sutures with surrounding elements along all but its mesial border. The resultant small dorsal aperture was thus well placed for surface breathing. In common with other primitive labyrinthodonts (Panchen 1967) a large nasolabial groove has developed to rid the naris of water. The large cartilaginous nasal capsules on the other hand may represent a specialization of loxommatids. The suggested contours in *M. pachycephalus* and *B. planiceps* are of unusually elongate structures extending back to the sphenethomoid, as in modern Amphibia. Undoubtedly olfaction was important and if the capsules could be air-filled they would function as flotation chambers, tilting the narial region up, possibly enabling the animal to 'hang' at the water surface.

The most puzzling feature of the loxommatid skull are the antorbital vacuities. No part of the structure housed the eye, since the extent of the orbit is indicated by the prefrontal flange from which the lachrymal duct originates ventrally. Romer (1947) suggested that the vacuity housed a glandular structure. Since in *Megalocephalus* this would be almost three times the size of the orbit and known orbital glands are either lachrymal or salt-secreting, such excessive development would be improbable in a fresh-water animal. An antorbital vacuity, believed originally to have developed in relation to a nasal salt gland, is described in the archosaur reptiles *Sphenosuchus* (Broom 1927) and *Euparkeria* (Ewer 1965). Since such glands are dermal in origin, such vacuities are formed as a concavity from the dorsal surface. The reverse is true for loxommatids, indicating development in relation to an internal structure and their form compares best with the temporal muscle fenestrae of early reptiles.

Of the muscles of the eye itself only the superior and inferior oblique originate around the front of the eyeball. These normally extend mesially and insert on the lateral wall of the brain-case. In loxommatids enlargement of the eye musculature could neither account for the size

or shape of the fenestration, nor for its highly modified lateral wall. The answer seems to lie in the method of jaw closure.

The successful capture of relatively large prey in water would necessitate jaws that could open widely and also powerful muscles to snap them rapidly shut from an open position against water pressure, although the latter was presumably compensated for to some extent by a synchronized depression of the hyoid, retaining water in the buccal cavity. The securing and possibly killing of prey would require the exertion of continuous muscle power as the jaws closed, in order to drive the teeth into the quarry. These two requirements would be achieved by the arrangement of the adductor musculature.

In primitive tetrapods the adductor mandibulae is usually considered to be divisible into three distinct masses (Romer 1956). The bulk of the muscle forms the external adductor, which primitively originated on the palatoquadrate, passing through the subtemporal fossa to insert on the mesial surface of the surangular region of the lower jaw in and around the margins of the adductor fossa. The posterior division was a short deep muscle descending from the quadrate region. The internal adductor of reptiles is divisible into the pseudotemporalis (which primitively would have had similar insertions to the external adductor mass) and, more important, the pterygoideus which extended well forward over the dorsal surface of the pterygoid and in early tetrapods is assumed to have attached posteriorly to the inner side of the jaw. In loxommatids, as in crocodiles, it is assumed that the pterygoideus muscle would be largely instrumental in effecting jaw closure. When the jaw was fully open the pterygoideus would be at its greatest mechanical advantage, acting approximately at right angles to a line joining the jaw joint and its point of insertion. Since successful predation required a relatively large, heavy jaw to be closed rapidly against water pressure, jaw closure would represent a kinetic inertial system (Olson 1961), as is assumed to be the case in the Rhipidistia (Thomson 1967) and in the anthracosaurs (Panchen 1970). In such a system the lower jaws were used in a 'sling' action, being accelerated from the open position with considerable force, complete closure relying on the kinetic energy acquired from the initial pull.

Structure of the antorbital vacuity and associated region suggest that a particularly large pterygoideus was a prominent feature of loxommatids. One would expect the pterygoideus to insert in the antorbital region, over the dorsal surface of the palatal elements (figure 26). The loxommatid skull is extremely shallow in this general area. The palate is fused to the skull roof around the level of the naris, since it forms the posterior wall of the anterior palatal fenestra. The sphenethmoid region of the braincase, against which the pterygoids abut, has in *Loxomma*, where it is best known, tapered to a depth of less than 1 cm at its extremity, about level with the tip of the antorbital vacuity. In such features the anthracosaur skull, with its strongly tropibasic ethmo-sphenoid region and deep snout, forms a sharp contrast. In crocodiles where the anterior part of the skull is relatively shallow the pterygoideus muscle bulges down into large palatal vacuities. In loxommatids, where there is a primitive solid palate, fenestration of the dermal skull roof would have allowed the muscles to bulge dorsally.

In his description of the archosaur *Stagonolepsis* Walker (1961) suggests that the margin of the antorbital fenestra in this form may have provided an area of origin for part of the pterygoideus mass. In loxommatids however it seems most likely that the fenestration merely represents a 'bulging hole' for the muscle, since the solid lateral wall of the vacuity has a smooth recurved surface, continued by the ventral jugal ridge back to the adductor fossa, against which the main body of the muscles would presumably contract.

In crocodiles, fibres of the pterygoideus muscle narrow into the 'stem tendon' which rolls over the lateral edge of the pterygoid flange and passes down to insert on the mandible (Iordansky 1964). In loxommatids the processus alaris of the jugal is well developed and may well have fulfilled a similar function to the pterygoid flange. Since the posterior margin of the ectopterygoid is not modified as a rolling surface, the large pterygoideus muscle could well have narrowed to a tendon in loxommatids also. This being the case the bulk of the muscle mass would be in the antorbital region, where considerable bulging must have occurred as the fibres contracted.

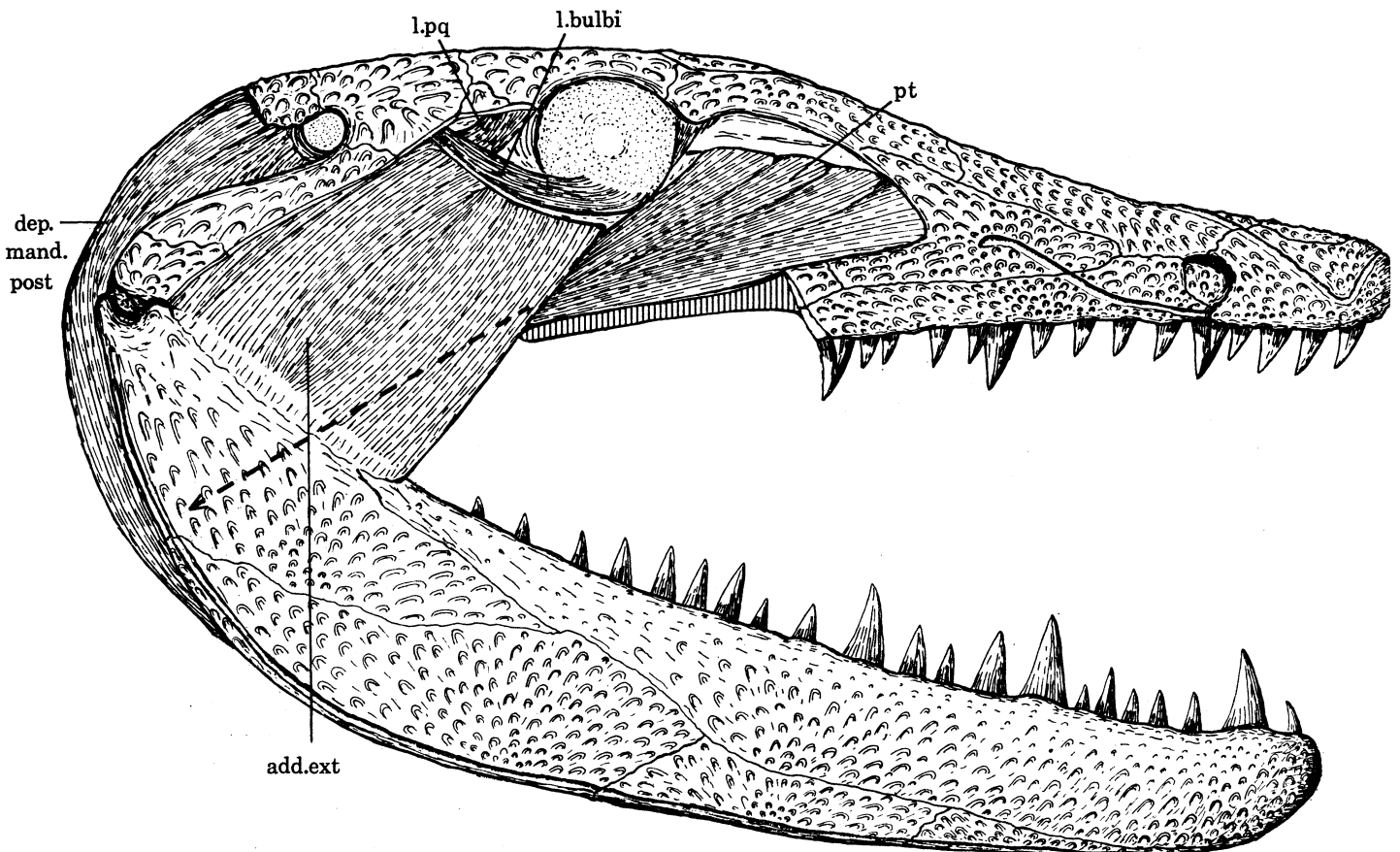


FIGURE 26. *Megalocephalus pachycephalus* (Barkas), skull in lateral view. Half natural size, reconstructed with jaw musculature: bones of cheek largely removed. The broken line indicates the line of action of the pterygoideus muscle which was probably reduced to a tendon lying mesial to the main external adductor mass.

Although instigated by the pterygoideus, complete jaw closure was presumably aided by contraction of a large external adductor mass. This would be at its greatest mechanical advantage as the jaw came into the almost closed position and would reinforce the power stroke, sinking the teeth into the prey. Consideration of this final action of jaw closure allows an explanation to be given of the function of the basal articulation in these primitive temnospondyls.

Thomson (1967) discussed the mechanics of the rhipidistian skull, in which movement at the basal articulation depended upon the kinetic nature of the skull and braincase. In Amphibia the rhipidistian intracranial joint, between the ethmosphenoid and otico-occipital portions of the braincase and skull table, has been obliterated, but in the majority of primitive labyrintho-

dents the basiptyergoid articulation between the braincase and the palatoquadrate is retained, in a form suggesting that mobility was still possible between these components.

Panchen (1964, 1970) has considered the mechanics of the skull of *Palaeoherpeton*. In this early anthracosaur the mobile articulation is considered as part of a kinetic mechanism involving mobility between the skull table and cheek region. He suggests that fibrous tissue in the supra-temporal-squamosal junction would serve as a compression member, minimizing forces on the quadrate region set up by the powerful jaw musculature. Such intracranial movements were thus dependent upon retention of the rhipidistian lateral kinetic zones in the skull roof and could only have occurred in anthracosaurs with this feature. In all temnospondyl Amphibia the skull table and cheek region are firmly united and yet the mobile basal articulation is primitively present. Thus, as noted by Thomson & Bossy (1970), the function of this joint in the supposedly solid temnospondyl skull presents a problem to which so far there has been no satisfactory explanation. Details of loxommatid skull structure now shed light on this enigma.

In the description of *Megalocephalus* (above) attention has been drawn to the various ways in which the bones are united. Interdigitating sutures often vary considerably between the dorsal and ventral surfaces and represent a strong immobile method of joining individual elements. When, on the other hand, sutures take the form of a simple overlap between adjacent bones they may represent areas of elasticity capable of accommodating slight distortion. If any larger movements are to occur a system of elastic ligaments or a synovial joint is necessary. On this basis it has been suggested that the loxommatid skull can be divided into two distinct units.

The dermal roofing bones are all firmly joined by interdigitating sutures. In many specimens a considerable degree of overlap was found to occur around the otic notch, sealing and strengthening the ancestral lateral kinetic zone. The minimum thickness of the roofing bone is around 1 mm in mature skulls, but it attains a depth of several millimetres in the skull table, around the skull margin and orbits and along the course of the lateral lines. The lateral tusk-bearing palatal elements are knit into the skull roof by thick cancellous bone, sandwiched between the dorsal and palatal periosteal layers. The braincase was fixed into the complex by cancellous bone and cartilage. No planes of weakness are apparent within the above unit and it is unlikely that any bone distortion would occur.

The remaining ossifications of the loxommatid skull, the palatopterygo-quadrate, are considered as the second unit. The pterygoid and epipterygoid were apparently united by cartilage in *Loxomma acutirhinus* and had largely co-ossified in *Megalocephalus pachycephalus* and would thus operate as a single sheet of bone, thickened only around the conical recess and where it met the sturdy quadrate ossification in an interdigitating suture. The average thickness of the pterygoid ossification over its palatal ramus is less than a millimetre, and in contrast to the dermal roofing bones, some flexibility of the palatal unit seems possible. The latter is fixed at its anterior end by an interdigitating suture with the vomers. All other sutures with the roofing unit, i.e. along palatine, ectopterygoid and squamosal, take the form of an overlap between adjacent bones. The presence of a specialized articulation between the quadrate and quadratojugal, described above for *Megalocephalus* (figure 11) completes the separation of the skull units posteriorly (figure 27 a). This hitherto unknown intracranial joint has important implications, since in these primitive temnospondyls there is potential for any movement occurring at the basal articulation to be accommodated in the main at this site, rather than by distortion of the entire skull structure, as has previously been assumed (Watson 1951; Thomson 1967).

Equally since a second articulation has developed in the loxommatid skull, it seems

reasonable to assume that some movement did occur at the basal articulation. As noted above, the only muscles capable of causing movement at this site are the external adductors, which primitively originated around the conical recess and the lateral surface of the quadrate ramus of the pterygoid–epipterygoid complex. These, as in crocodiles, are presumed to reinforce the power stroke as the jaws closed and would thus help kill or stun the prey. In a case of successful

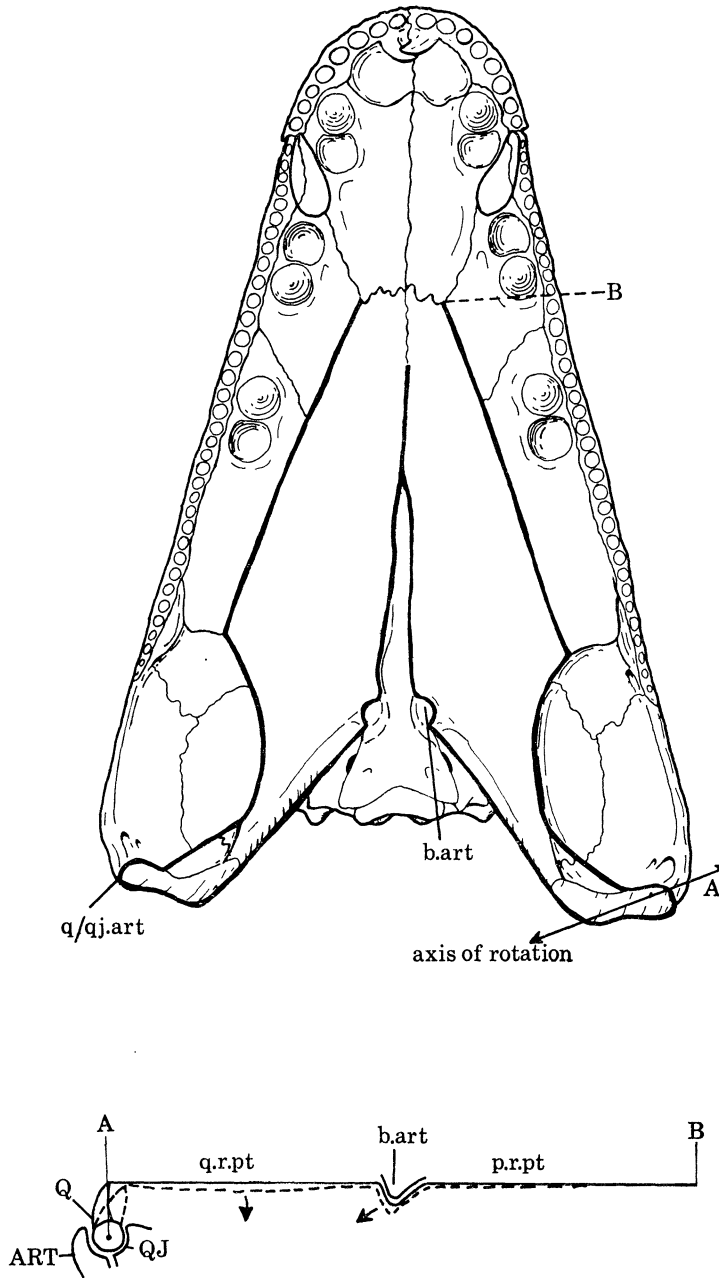


FIGURE 27. *Megaloccephalus pachycephalus* (Barkas). (a) Diagram of the palate to illustrate division of the skull into two units (see text). (b) Two-dimensional diagrammatic representation of movement of the palatal complex. It is postulated that in prey capture, contraction of the external adductor mass would cause the quadrate ramus of the pterygoid to bow laterally. Effective shortening in this region would be accommodated at the basal articulation and by rotation of the quadrate around its articular face with the quadratojugal. Thus the distance A–B remains constant and distortion is restricted to the thin palatal complex (see text).

prey capture, therefore, the progress of the lower jaw would be suddenly arrested at the moment when the reaction of the external adductor mass was most effective. It is assumed that under these circumstances the muscle would cause distortion of its thin attachment surface. Were the quadrate ramus of the epipterygoid complex thus caused to bow laterally, the conical recess would be pulled ventrally in a posterolateral direction, i.e. along the ridge formed by the articular surfaces of the basipterygoid process (described above for *Megalocephalus*). If such movements were to occur, the pterygoid ramus of the quadrate would be pulled anteriorly.

Owing to the complex nature of the quadrate articulation with the quadratojugal, it is possible that slight distortion, and thus in effect shortening, of the quadrate ramus could occur, whilst the overall length of the palatoquadrate (i.e. vomerine suture to jaw articulation) remained constant. Accommodation would take the form of a rotation around the articular surface with the quadratojugal. Since the latter represents a continuation of the normal articular face of the quadrate it may well have been a synovial joint. The principle of such intracranial movements may be most simply illustrated in two dimensions (figure 27*b*), although it must be appreciated that in fact the axis of rotation lies at right angles to the line of the palate and the plane of the pterygoid rotates through approximately 90° along its length (figure 27*a*).

The slight intracranial movements envisaged are thus such as may have occurred when the jaws were snapped shut with great force in prey capture. The levator palatoquadrati, the dorsal trigeminal muscle between the braincase and palatoquadrate, may have formed part of the corrective mechanism, pulling the palatoquadrate antero-mesially back to its original position, or possibly, were the basal articulation a ligamentous connection, the elastic energy of the system would be self-correcting.

Correction of torque around the quadrate may have synchronized with the slight change in orientation of the articular when the jaws were completely closed. From the structure of the lower jaw rami (figures 14, 15), jaw closure also involved movement of the pair at the symphysis, since this region was unfused and apparently packed with elastic ligamentous tissue. When the gape was at its widest it would appear, from the nature of the articular region, that the jaw rami were splayed out slightly, possibly due to contraction of the mylohyoideus musculature. In such a position the teeth would incline slightly outwards. However, as the jaws closed the teeth would be pulled back into a vertical plane, due to tension of the symphyseal ligaments.

Such movements of the lower jaw rami were accommodated by the nature of the jaw articulation described above for *Megalocephalus*. The articular has a long crescentic glenoid fossa, which dips slightly towards its anterior margin. The corresponding articulating face of the quadrate mirrors the glenoid fossa and forms a broad band which rotates through approximately 180° along its transverse length. Thus, at the postero-lateral extremity of the condyle, the articular surface faces posteriorly. It then extends around the condyle so that in the anterior region it faces laterally. When the gape was wide the glenoid fossa would have a dorso-lateral orientation and only the posterior two-thirds of the quadrate condyle would be applied to it. Only when the jaws were completely closed and the fossa assumed a dorsal orientation could the quadrate rotate into the glenoid along the whole of its length.

A similar system operated in the anthracosaur jaw and Panchen (1972) suggests that their spring system around the symphysis may have been important in bringing the dentary teeth into their correct alignment, between marginal and palatal teeth, as the jaws snapped shut. It seems likely that, although the same may be true of loxommatids, mobility at the jaw

symphysis developed as part of a more general system to allow accommodation at regions where considerable tensile stress was likely to occur.

Loxommatids, in common with other Palaeozoic Amphibia, inherited from rhipidistian ancestors a thin palatal complex, with the basal articulation as its major point of contact with the braincase. Were the basal articulation to suture up, whilst the jaw muscles retained their primitive origin on the palatoquadrate, there would be considerable danger of shear at this point as the jaws snapped shut. The basal articulation would thus function as a zone of elasticity at the region of maximum tensile stress. In loxommatids, as the lateral kinetic zone had sealed early, the rhipidistian contact surface between the quadrate and cheek became modified as the means of accommodating the slight movements involved. In addition the overlap surfaces between the pterygoid and adjacent elements, being presumably sealed by elastic cartilage or connective tissue, would restrict bone distortion to specialized movements within the thin palatal complex. Thus the system described for these primitive temnospondyls may be considered as an alternative design to that of the anthracosaurs where the mobile cheek region is primitively retained to accommodate the stresses on the skull caused by a powerful jaw musculature.

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LIST OF ABBREVIATIONS USED IN THE TEXT-FIGURES

A	angular	p	parietal
add. ext	external adductor muscle	p.a.f	posterior angular foramen
ART	articular	PAL	palatine
BO	basioccipital	par.pr	paroccipital process
b. art	basal articulation	PF	postfrontal
b.pr	basipterygoid process	PMX	premaxilla
BSP	basisphenoid	PO	postorbital
car. f	carotid foramen	POSL	postsplenial
ch	choana	PP	postparietal
col. cr	columella cranii	pr.al	processus alaris
con. rec	conical recess	PR.ART	prearticular
COi	anterior coronoid	pr.cul	processus cultriformis
Coi	middle coronoid	PRF	prefrontal
COiii	posterior coronoid	PRO	pro-otic
D	dentary	p.r.pt	palatal ramus of pterygoid
dep.mand. post	posterior depressor mandibuli muscle	psp	parasphenoid
ECT	ectopterygoid	PT	pterygoid
EPT	epipterygoid	pt	pterygoideus muscle
ept. fac	facet for epipterygoid	p.te.fs	post-temporal fossa
EO	exoccipital	Q	quadrate
eo. fac	facet for exoccipital	q/qj art	articulation between quadrate and quadratojugal
fen. ov	fenestra ovalis	QJ	quadratojugal
F	frontal	SA	surangular
f. mag	foramen magnum	SL	splenial
f.p.q	paraquadrate foramen	SMX	septomaxillary
f.p.q.a	accessory paraquadrate foramen	SPET	sphenethmoid
i.c.	intercentrum	SQ	squamosal
i.car	internal carotid artery (course of)	ST	supratemporal
IN	internasal	st	stapes
IT	intertemporal	st (gr)	groove marking position of stapes
J	jugal	st.gr	groove for stapedal process to quadrate
L	lachrymal	T	tabular
l.bulbi	levator bulbi muscle	t.fac	facet for tabular
l.pq	levator palatoquadrati muscle	V	vomer
MX	maxillary	v.c.dor	vena capitis dorsalis (course of)
N	nasal	Nerve foramina in the skull are indicated by Roman numerals: I, olfactory; Ivm, vomeronasal; II, optic; III, oculomotor; IV, trochlear; V ₁ , profundus; V ₂₊₃ , trigeminal; VI, abducens; VII, facial; VIII, auditory; IX, glossopharyngeal; X, vagus; XI, accessory; XII, hypoglossal.	
nlb.gr	naso-labial groove		
nld	naso-lachrymal duct		
OP	opisthotic		
o.cap	otic capsule		
op. fac	facet for opisthotic		
o.pr	otic process		

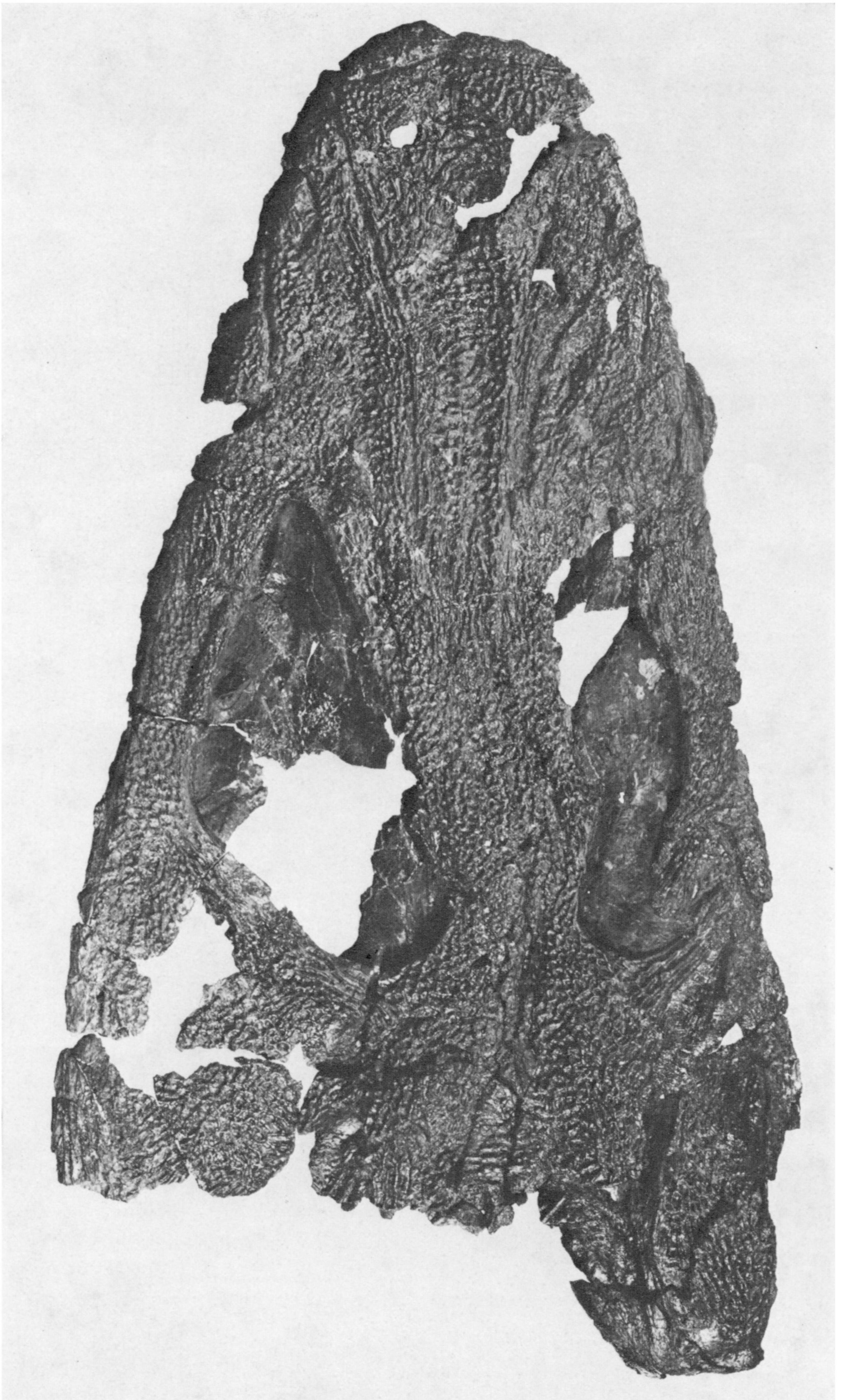


FIGURE 6. *Megalocephalus pachycephalus* (Barkas), holotype skull in dorsal view. Half natural size.

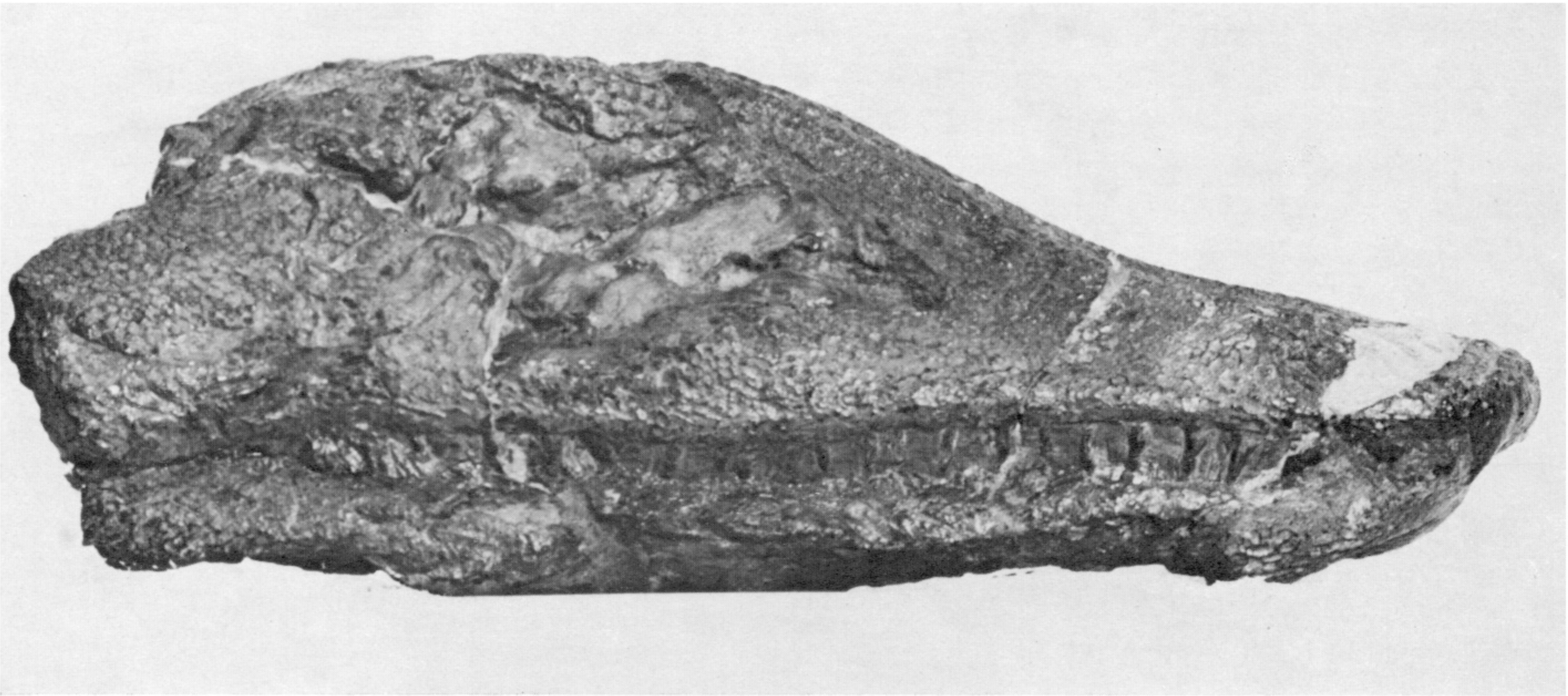


FIGURE 7. *Megalocephalus pachycephalus* (Barkas), Coalbrookdale skull.
B.M.(N.H.) R585 in right lateral view. Half natural size.